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ECOLOGY OF THE MOSSES OF GRAND DE TOUR REGION OF ILLINOIS, WITH SPECIAL REFERENCE TO pH RELATIONS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 414

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Introduction

Work on soil reactions with respect to plant distribution has progressed greatly during the last few years. In a short review, WHERRY (31) states that although the first paper on soil reactions and natural plant distribution appeared in 1916, during the following decade more than 500 papers were published on this general subject. Among early workers, HEALD (11) found that the positive ion of weak acids and soil salts produced a toxic effect on seedlings. Following this lead, many theories concerning the causes of soil acidity were rapidly developed. HARRIS (9) reviewed these in 1914, and suggested that soil acidity was due to the fact that colloids adsorbed the negative ions from soil salts, leaving the positive ions to give the acid effect. WHERRY (26) described soil acids as both organic and inorganic, and indicated that colloids were indirectly effective.

The importance of total soil acidity soon gave way to the idea of H-ion concentration. GILLESPIE (5) discussed acid intensity, H-ion concentration, as a more potent factor in plant growth than total acidity. WHERRY (25, 27–30) has demonstrated the effect of the H-ion concentration upon many of the various groups of the higher plants. KURZ (14) showed the H-ion to be an important ecological factor in the different soils of the Chicago region. SALISBURY (19)

found that in old forest soils the top layer contained the higher H-ion concentration, which decreased in the lower layers and finally became alkaline. The alkaline materials of the top layers leach more readily than the acid and are therefore carried to the lower strata, leaving the acids above. Thus soils in different places show the variable reaction which is a basic factor in plant distribution. OLSON (17) found that as a rule the availability of some soil nutrients is not affected by the H-ion, and therefore the H-ion concentration itself is an important factor in plant groupings. Although WHERRY discovered that northern ferns generally prefer alkaline soils and southern ones prefer acid, STEAGALL (22) did not find that the ferns of Illinois showed these preferences. ROSEN (18) found a bacterial disease of foxtail sensitive to the H-ion concentration of the media.

Some experimenters have taken a slightly different angle of the problem. HARTWELL (10) noticed that the sap of flat turnips was more acid when grown in soils of a higher phosphorus content. TRUOG (24) states that alkaline substances of the soil caused plants to have higher alkaline contents. HABER (8), working with the tomato, found that the contents of the plant were affected proportionately to the acid or alkaline substances of the soil. The roots seemed to be most affected and the fruits least.

There is less literature on mosses in relation to the H-ion concentration. SKENE (20) found sphagnum sensitive to acids and bases both in substrata under natural conditions and in artificial cultures. KURZ (15), working on bogs, concluded that sphagnum and associated mosses were the cause of bog acidity. His conclusions were based on the fact that bogs where these mosses had not appeared were not acid but alkaline in reaction. AMANN (1) classified mosses as acid, subacid, neutral, and alkaline. He used the colorimetric method to test the soils, but there is no indication concerning the accuracy of his work. TAYLOR (23) studied the succession of mosses on various habitats in the Chicago region, and found an interesting correlation from this angle. DAVEY DE VIRVILLE (2) studied the relation of mosses to environment. He experimented on such ecological factors as sunlight, water, temperature, humidity, and soils, but did not touch upon the H-ion concentration.

The purpose of the investigation here reported was to discover the

H-ion concentration relationships between the mosses and their substrata in the region of Grand de Tour, Illinois, this vicinity offering a good variety of both mosses and habitats. In the beginning it was thought necessary to make tests only of the top centimeter of soil and the moss parts that lay upon the surface, but later it was found desirable to add readings of the soil 2-3 cm. deep. The first group of tests included such materials as moss bases, rhizoids, humus, and soil particles; the second group usually consisted of soil materials only, exclusive of moss parts and humus. In the original plan the intention was to gather data that would show to what extent if any the mosses affected the H-ion concentration of the soil. From evidence accumulated in this work, and from the work of KURZ (**15**), it seems likely that there is a contribution to the soil from the moss, but upon further study it was found that data gathered in this way could not be used in the solution of the problem. This part of the work had to be abandoned therefore, since it required a special method and a much longer time than the other parts of the program.

Finally the work resolved itself into the four following phases: (1) to discover the H-ion concentration of the mosses and the top soil to which they were attached; (2) to discover the H-ion concentration of the soil 2-3 cm. deep; (3) to see whether there was any correlation between (1) and (2); (4) to determine the H-ion range of some of the more common mosses of the region. The work on the last part was necessarily limited, because in making the tests the mosses were taken as they naturally occurred in the field, and no effort was made to get a certain large number of tests for any moss or group of mosses.

Investigation

METHODS

With the exception of a few samples brought to the laboratory for checking, all tests were made in the field. The Morgan Soil set (**16**) was used throughout to test both the soils and moss materials. This is a colorimetric tester developed to an accuracy of 0.2 pH. It consisted of a porcelain block arranged in such a manner that when the soil was placed in part of a groove the indicator could be dropped into another place and allowed to run through it into a small pit. A color chart was then used to read the results. The indicators em-

ployed in this apparatus were phenol red, bromthymol blue, chlorphenol red, and bromcresol green. The complete range of the set was from 8.2 in phenol red to 3.8 in bromcresol green. At first tests were made of the top soil and the moss materials on the surface, but later tests of the soil 0.5-1 inch deep were also taken. If there was any doubt about the results in any case the test was repeated until a constancy was reached. In order to insure greater certainty, tests were made in the field, in the laboratory, and in both wet and dry conditions. Check tests were also made of the same plot at different times throughout the season. Moss samples were collected and brought to the laboratory for identification. The manuals of GROUT (**6, 7**) and DUNHAM (**4**) were used in this work.

All readings were taken in pH values because the color charts were marked in those figures. Thus the color chart for bromcresol green read 3.8-4.0-4.2-4.4-4.6-4.8-5.0-5.2-5.4-5.6, and the others followed the same scheme with a slight overlap on the indicator to each side. The pH values translated to units of H-ion concentration are as follows: the pH value of 3 equals the H-ion concentration of 0.001 (gm. H per liter), 4 is equal to 0.0001, 5 to 0.00001, 6 to 0.000001, 7 to 0.0000001 (the neutral point), and 8 to 0.00000001 (an alkaline reaction). Altogether there were a few over 1100 recorded tests. These are charted and listed in such a manner as to show the pH range of each area studied and the pH range of the different species found. In connection with the latter point, there were many species for which so few readings were taken that these can be considered only suggestive and not in any way conclusive.

GRAND DE TOUR REGION

The field covered in this survey included the Rock River bluffs and valleys in the vicinity of Grand de Tour, Illinois, some bluffs near Castle Rock and the Devil's Backbone, and the Illinois State Park known as The Pines. These places are all in the region called the Dixon quadrangle, as described by KNAPPEN (**13**) of the Illinois State Geological Survey. The region offered a wide variety of geological and ecological situations, such as gentle slopes, steep hillsides, valleys, open spaces, wooded spots, flat hill tops, and faces of hillsides in almost every direction. From a geological point of view the

region has exposures of St. Peter sandstone, Platteville limestone, and the Illinois glacial moraine. These materials are in various stages of erosion and are more or less mixed with humus from the plant cover.

St. Peter sandstone and the eroded sand from it form the basic soil for all the territory near Grand de Tour, Castle Rock, and the Devil's Backbone. This is found in open exposures and with different types of cover. It is in the realm of the oak-hickory climax and these woods occupy practically all the places studied. The north slopes and other protected places are usually coated with a layer of humus of varying degrees of thickness. These are in various stages of mesophytism and are covered with a wide variety of higher plants as well as mosses. Rock and sand outcrops are frequent, both on the tops of bluffs and hillsides. Such places are xerophytic and support a sparse vegetation.

The Pine Woods is a remnant of native white pine timber that has not only been able to maintain itself against the competition of other species, but is actually reseeding the parts that have been occupied by the oaks. The trees are rooted in a shallow layer of Illinois glacial till of varying depths. This overlies Platteville limestone which outcrops in the bluffs along Pine Creek. The creek has cut a deep valley through the park, forming steep bluffs that give a variety of places for the growth of plants. The pines begin at the top edge of the east bluff and extend eastward in varying widths throughout the length of the park. Oak-hickory woods occupy a large portion of the rest of the region. The east bluff is very mesophytic, and is covered with a thick growth of vegetation except in small sections of a vertical cliff. The west bluff is drier and has much more rock exposure. Cedars are prominent trees along this bluff.

This region lies in the cool temperate belt and has an average annual rainfall of 30–35 inches. The annual mean temperature is around 45° F. Climatic changes are often sudden and at times severe, but not so hard that the ordinary vegetation for this region ever fails to develop. DeForest (3) presented data on precipitation and temperature over a period of 62 years. He thought that during that period there was a slight drop in precipitation, but otherwise no noticeable change in climatic conditions.

BABSON HOLLOW

In the woods along the river northwest from Grand de Tour, a small stream has cut a deep valley in the ridge parallel to the river edge. It runs in a westerly direction for a short distance, forming a typical mesophytic north-facing bluff about 50 feet high. This bluff is covered with oaks, walnuts, elms, and cherries. In the spring hepaticas, bloodroots, trilliums, claytonias, and many other common wood plants are abundant. Throughout the growing season parts of this slope are well matted with luxuriant growths of mesophytic mosses. Many of them scarcely check their growth through the drier months of summer, because of the very regular supply of water. Evaporation rates are always low because sun and wind have no chance to reach this secluded spot. In many places the mosses are in a pure stand while in others they represent a wide variety of mixtures.

At the top of the bluff, in an open place covering several square yards, are a few patches of *Polytrichum commune* and *Catharinea angustata*. These mosses are growing luxuriantly and are found in practically pure stands. Small bits of forest débris have settled among them, but not enough to interfere with their normal growth habits. This is the driest part of the whole plot, owing to the fact that the moisture supply is not so good as farther down the hillside and evaporation is more rapid. On this account growth ceases during the dry parts of the season.

Farther down the hillside different groups of mosses appear. Those that occur most commonly are *Catharinea undulata*, *Bartramia pomiformis*, and *Aulacomnium heterostichum*. In places they extend well to the bottom of the slope. *Bartramia* is especially abundant in the steeper shaded areas in both pure stands and mixtures. These mosses are rather hardy, and are prominent throughout the growing season. Other mosses that grow luxuriantly at different parts of the season are *Mnium cuspidatum*, *M. hornum*, *Hylocomium triquetrum*, *Thuidium recognitum*, *Eurhynchium serrulatum*, *Brachythecium oxycladon*, and *B. rutabulum*. *Eurhynchium* and *Brachythecium* occur all the way to the bed of the stream and may be found on soil and dead wood alike.

The underlying soil of this slope is St. Peter sandstone. In places it is covered with a layer of humus on which the mosses grow; in

others the moss mat is directly upon the sand and forms its own layer of humus. The source of water is not only from precipitation but from seepage and capillary movement. These give an ample supply which is well conserved for the heavy plant cover.

The H-ion concentration on this slope was characteristic of hillsides in general. Near the top, in the more or less level beds of *Polytrichum* and *Catharinea angustata*, the moss tests ran between 5.0 and 6.0 and the soil 1 inch deep held between 4.0 and 5.0. Farther down the slope, in mixed beds of *Aulacomnium*, *Hylocomium*, *Bartramia*, and *Mnium cuspidatum*, the moss tests rose to a range from 6.4 to 7.6, while soil tests rose to 5.2. At the foot of the bluff and in the stream bed the moss tests reached 8.0 and 8.2, but the soil gave tests from 6.0 to 8.0. The entire range for the mosses on this slope

TABLE I

BABSON HOLLOW; pH TESTS OF MOSSES AND TOP SOIL

| SPECIES | RANGE OF pH | | |

stone which is badly eroded into pockets, shelves, and crevices of many descriptions. In most places loose sand covers the rock, but at times the crumbly rock is bare. The top edge of this bluff is semi-xerophytic and for this reason was included in this study. Thin layers of humus have accumulated in pockets and other protected spots. Disintegration and erosion are rapidly changing the surface layers in many places. These features, together with the dry conditions, make an unfavorable situation for moss growth.

Vegetation along the edge of this bluff is not dense. Oaks and hickories are the dominant trees, with a fringe of junipers occupying the more exposed and difficult sites. Few of the herbaceous forms find a place to lodge. *Draba* sp. may be found along the shelves and paths, and *Viola pedata* is widely scattered over the slope above. On the more level spots *Amphicarpa monoica* attains a moderate growth in the late summer. There are no dense coverings of any kind and all plants reach only an average size. Mosses find this a difficult place in which to get a foothold. Some have been able to lodge on the narrow rock and sand ledges, and others have become well established on the stable surfaces under trees and in the more protected pockets. Although *Polytrichum commune* and *Catharinea angustata* have been able to spread over rather large patches, other mosses are found only in small clumps. None of the species have made the growth here that they have in more mesophytic places. Under the cedars and in more protected spots were well developed mats of *Brachythecium oxycladon*. This moss has a liking for neutral to alkaline soils, and on the sandy soil of this bluff maintains a range from pH 7.0 to 8.2. Sand shaken out of the rhizoids tests 7.0 and 7.2, but 1-inch deep tests range between 5.0 and 6.0. Other mosses occurring on this bank are *Catharinea undulata*, *Pohlia nutans*, *Mnium spinulosum*, *Bryum binum*, *B. argenteum*, *B. caespiticium*, *Encalypta ciliata*, and *Ceratodon purpureus*.

The pH readings of this region showed a wide variation and an unusual irregularity. *Polytrichum commune* ranged from 5.0 to 7.4, and *Catharinea angustata* varied from 6.0 to 8.0. Vertical slopes covered with *Mnium spinolosum*, *Encalypta ciliata*, or *Brachythecium oxycladon* were always neutral or alkaline, but if *Pohlia nutans* or *Dicranum scoparium* formed the moss cover the tests were regularly

acid. The entire range of this bluff for the mosses and top soils was 4.6–8.2; for the soils 1 inch deep it was 4.2–7.2. A complete list of the mosses found in this area with the range of their tests is given in table II.

TABLE II

Species	Range of pH	
	Moss and top soil test	Test of soil 1 inch deep
Brachythecium oxycladon	6.0–8.2	5.0–7.4
Bryum argenteum	7.6–8.2	8.0
Bryum roseum	7.6	7.4
Bryum caespiticium	5.4–7.6	6.2
Bryum binum	8.0	.....
Mnium spinulosum	6.4–7.2	.....
Catharinea angustata	6.0–8.0	5.6–7.4
Polytrichum commune	5.2–7.4	5.6–6.2
Barbula unguiculata	7.4	.....
Tortula ruralis	7.8	.....
Ceratodon purpureus	4.6–7.6	5.2–5.6
Encalypta ciliata	7.6	.....
Pohlia nutans	5.2	.....
Dicranum scoparium	4.4–6.0	4.4
Ditrichum pallidum	7.4	6.2
Funaria hygrometrica	7.4	6.2
Thelia lescurii	7.0–7.2	7.2

Black Hawk Bluffs.

South and west of the county line bridge below Grand de Tour are three large moss plots that present very different situations. One is a dry hilltop with a mesophytic slope, another is a mesophytic shelf on the north side of a steep bluff, and the third is a wet hillside.

A few rods west of the bridge close by the river is a prominent outcrop of sandstone. The top is dry and open, with only a thin layer of sand covering a part of the rock. On the eastern edge are a few dwarf oaks, and on the north and west edges are some straggling specimens of *Pinus strobus* and *Betula lutea*. Huckleberries are able to find rooting in the large cracks of the rock, and *Draba* sp. and *Viola pedata* are the most common species of herbaceous plants. The south slope is gradual and not difficult of approach. Characteristic plants are *Ranunculus fascicularis*, *Antennaria alternifolia*, *Draba* sp., *Viola pedata*, *Synthyris bullii*, and a few hardy grasses. The east slope from the base almost to the top is mesophytic. *Quercus rubra*

and *Hamamelis virginiana* form the tree covering, and vigorous plants of *Arisaema triphyllum*, *Smilacina* sp., *Hepatica triloba*, and *Aralia nudicaulis* are the most common smaller forms.

At the foot of the east side the most widely distributed moss was *Mnium cuspidatum*. Other mosses that occurred in scattered patches were *Bryum caespiticium* and *Brachythecium oxycladon*. These mosses ranged from 7.4 to 8.2, and grew on a substratum that tested from 6.8 to 7.0. Near the middle of the hill were large mats of *Thuidium recognitum*, *Catharinea undulata*, and *Polytrichum commune*. These grew on thin layers of sand and over the edges of rock shelves. They ranged from 5.4 to 8.2. On the ledges and the summit of the bluff the species that occurred most frequently were *Polytrichum commune*, *P. piliferum*, *Catharinea angustata*, *Pohlia nutans*, and *Dicranella heteromalla*. The range was 4.2–7.8 while the substratum tested 4.4–7.2. Some noticeable irregularities occurred on this bluff. *P. piliferum*, which usually grew on highly acid soils, tested 7.2 on sandy soil with a range of 5.0–7.2. *C. angustata* tested 7.4 on soil of 7.0; *P. commune* and its soil both ran to 7.2. On the south slope were some large plots of *P. commune* mixed with a few specimens of *Thuidium recognitum*, *Bartramia pomiformis*, and *Brachythecium oxycladon*. These all tested from 7.2 to 7.8 and the soil ran 4.4–7.2. The tests of the soil usually ran about 7.2, but one spot was found in which the tests were 4.4.

These irregularities are probably caused by different water movements through the rocks and soil. In some places the water comes out as seepage from the layers above, giving a soil with an alkaline reaction. In others the water runs down through the soil, leaving acid conditions at the surface. A few rods south of this bluff is a steep hillside about 45 feet high covered with a thick carpet of mosses. Through the season water seeps down this hill, giving a good supply of moisture to the moss cover. Close around the moss bed are such plants as *Thalictrum dioicum*, *Smilacina* sp., *Hepatica triloba*, *Geranium maculatum*, and *Sanguinaria canadensis*. Trees grow near, so that direct sunlight does not fall upon the moss bank for any length of time during the day.

The base of the slope is well covered with *Catharinea undulata* intermixed with *Conocephalus* and *Bartramia pomiformis*. From 6 to 10 feet up *Catharinea* gives way to *Bartramia* and *Thuidium recog-*

nitum. Higher up *Mnium cuspidatum*, small clumps of *Polytrichum commune*, *Aulacomnium heterostichum*, *M. hornum* and *Anomodon attenuatus* complete the cover. These belts are adjusted rather closely to the moisture supply of the hill, with the drier part at the top.

Most of the pH tests of the mosses on this bank were alkaline. In one small plot of *Bartramia*, *Thuidium*, and *Polytrichum commune* the tests were 5.8 to 6.6, but all the others ranged from 7.0 to 7.8. Soil tests ranged from 6.0 to 7.0. The soil below these mosses was almost pure sand with a thin layer of humus formed by the mosses themselves.

A few rods farther south of this same bluff is another moss bank of a different type. It is a broad talus shelf with vertical cliffs above and below. The soil is pure sand held in place by moss beds and humus from the trees. It is a north slope completely shaded by oaks and the cliff above. The north edge is bordered by a number of scrubby pines.

The most interesting moss on this shelf was a luxuriant bed of *Climacium americanum*. A large patch and several small ones had become established near the base of the shelf. *Polytrichum commune* also grew well in the surrounding spaces. Other mosses found on the slope and cliff above were *Catharinea angustata*, *C. undulata*, *Pohlia nutans*, *Mnium cuspidatum*, *Bartramia pomiformis*, *Aulacomnium heterostichum*, *Thuidium recognitum*, and *Brachythecium oxycladon*. These showed their usual reactions when tested. *C. angustata* ran 5.2 on soil with the same test; *P. nutans* tested 4.6 on a sand wall of 4.2; *P. commune* ranged from 6.4 to 7.0 and the soil 1 inch deep tested from 5.4 to 7.0; *Climacium americanum* tested from 6.6 to 7.6, and the soil below ran from 5.2 to 7.0. Other mosses ranged 7.2–7.6 with soil tests varying from 4.8 to 6.8. Although the moss tests were rather regular the soil seemed to be more widely variant. The correlation between the mosses and soils was close in some cases but in others there was a wide difference (table III).

Tree mosses

Tree mosses in the Rock River region were not abundant nor vigorous. Three widely separated groups of trees were found to have somewhat representative species, and a brief survey of these was taken.

One wood, an old floodplain along the Black Hawk bluff, is a region of the mesophytic type. The common trees are *Ulmus americana*, *Celtis occidentalis*, and *Juglans nigra*. These are scattered so that there is plenty of sunlight for the grass cover underneath. The soil is chiefly a sand till washed in from the bluff above, mingled with silt and humus. A few partially decayed stumps and old logs made good substrata for mosses. On tree bases, old wood, and soil surrounding them are such species as *Anomodon minor*, *Amblystegiella adnata*, *Brachythecium oxycladon*, *B. rutabulum*, and *Mnium cuspidatum*. The pH tests for mosses and their substrata were all alkaline, ranging 7.0–7.8. This is the usual condition for areas of this kind.

TABLE III

Species	Range of pH	
	Moss tests	Test of soil 1 inch deep
Polytrichum commune	5.0–7.4	4.4–7.4
Polytrichum piliferum	5.6–7.4	5.0–6.2
Catharinea angustata	5.4–7.4	5.4–6.0
Catharinea undulata	6.0–7.6	5.4–6.8
Ceratodon purpureus	7.4	6.4
Dicranella heteromalla	4.8	.....
Pohlia nutans	4.2–4.6	4.2
Aulacomnium heterostichum	7.4–7.8	5.2–5.4
Bartramia pomiformis	7.2–7.8	5.4–6.0
Bryum argenteum	8.2	.....
Mnium cuspidatum	7.6	5.4
Mnium hornum	7.4	.....
Thuidium recognitum	5.8–7.4	4.8–7.4
Anomodon attenuatus	7.0–7.8	7.0–7.2
Brachythecium oxycladon	7.4–7.6	5.2–7.2
Climacium americanum	6.4–7.8	5.2–7.2
Entodon cladorrhizans	7.4	8.2
Pylaisia schimperi	7.4	.....

The uplands behind the floodplain have been cleared of underbrush and are occupied by pasture grasses. Oaks and hickories are left standing but do not interfere with growth of the grasses. The soil is sand mixed with a small amount of silt and humus. Mosses grow generally on the soil but some are found on the bases of the trees. Those occurring most frequently are *Anomodon attenuatus*, *Brachythecium oxycladon*, *Ceratodon purpureus*, and *Polytrichum commune*. The pH readings of the mosses ran 7.4 and 7.6 on soil that tested from 5.4 to 6.8.

About one mile to the southeast of the county-line bridge is a small open group of trees (oaks and hickories) supporting a few tree mosses. The soil is a gravelly till from the Illinoian ground moraine, sloping gently to the northwest and covered with a thin layer of leaf humus. Mosses find a footing on the soil, tree bases, old logs, and stumps. The most abundant species are *Anomodon attenuatus*, *Amblystegium serpens*, *A. kochii*, *A. adnatum*, *Entodon cladorrhizans*, and *Mnium cuspidatum*. The tests for the mosses, bark, and soil ranged 7.2–7.6 except in one case where the moss and bark went to 6.8.

The third wood studied for tree mosses was a portion of the eastern part of the pine-oak mixture at The Pines. Part of the work was in a thick growth of oaks with a heavy undercover, part in open timber, and the rest in a thick group of young pines. The soil was sand and gravelly till of the Illinoian ground moraine, covered generally with a layer of humus. In the oaks *Psedera quinquefolia*, *Celastrus scandens*, *Galium* sp., and many other forms hid the ground except in spots. Under the pines needles made such a thick coating of humus that few other plants could get a start. On tree bases, old logs, and stumps among the oaks were found *Mnium cuspidatum* and *Amblystegium serpens*. These tested from 7.0 to 8.2 on soils testing from 4.8 to 7.0. In the young pines the mosses were confined to the bases of trees and barren soils. The prevailing species were *Brachythecium rutabulum*, *Amblystegium serpens*, *Amblystegiella adnatum*, *Bryum roseum*, and *Catharinea undulata*. Tree mosses tested from 6.8 to 7.6 and soil mosses ran between 5.4 and 6.4. The pH of the soil under these pines varied from 4.0 to 7.0. A few small clumps of *Dicranella heteromalla* at the base of the larger pines ran to 4.4 on soil with a pH of 4.2. In all cases where a moss was found both on tree base and soil the soil specimen tested more acid. One case of *A. adnatum* on the bark of a pine showed a reading of 5.4, which is unusually low for tree mosses. In general these tests showed that tree mosses of this region were from neutral to the limit of the alkaline scale. Individual tests in other plots corroborated these data (table IV).

Pine Woods

About 6 miles east of Polo, where the Burlington Railroad crosses Pine Creek, is the last important vestige of native white pines of north-

One wood, an old floodplain along the Black Hawk bluff, is a region of the mesophytic type. The common trees are *Ulmus americana*, *Celtis occidentalis*, and *Juglans nigra*. These are scattered so that there is plenty of sunlight for the grass cover underneath. The soil is chiefly a sand till washed in from the bluff above, mingled with silt and humus. A few partially decayed stumps and old logs made good substrata for mosses. On tree bases, old wood, and soil surrounding them are such species as *Anomodon minor*, *Amblystegiella adnata*, *Brachythecium oxycladon*, *B. rutabulum*, and *Mnium cuspidatum*. The pH tests for mosses and their substrata were all alkaline, ranging 7.0–7.8. This is the usual condition for areas of this kind.

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Ceratodon purpureus	7.4	6.4
Dicranella heteromalla	4.8	.....
Pohlia nutans	4.2–4.6	4.2
Aulacomnium heterostichum	7.4–7.8	5.2–5.4
Bartramia pomiformis	7.2–7.8	5.4–6.0
Bryum argenteum	8.2	.....
Mnium cuspidatum	7.6	5.4
Mnium hornum	7.4	.....
Thuidium recognitum	5.8–7.4	4.8–7.4
Anomodon attenuatus	7.0–7.8	7.0–7.2
Brachythecium oxycladon	7.4–7.6	5.2–7.2
Climacium americanum	6.4–7.8	5.2–7.2
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Pylaisia schimperi	7.4	.....

The uplands behind the floodplain have been cleared of underbrush and are occupied by pasture grasses. Oaks and hickories are left standing but do not interfere with growth of the grasses. The soil is sand mixed with a small amount of silt and humus. Mosses grow generally on the soil but some are found on the bases of the trees. Those occurring most frequently are *Anomodon attenuatus*, *Brachythecium oxycladon*, *Ceratodon purpureus*, and *Polytrichum commune*. The pH readings of the mosses ran 7.4 and 7.6 on soil that tested from 5.4 to 6.8.

About one mile to the southeast of the county-line bridge is a small open group of trees (oaks and hickories) supporting a few tree mosses. The soil is a gravelly till from the Illinoian ground moraine, sloping gently to the northwest and covered with a thin layer of leaf humus. Mosses find a footing on the soil, tree bases, old logs, and stumps. The most abundant species are *Anomodon attenuatus*, *Amblystegium serpens*, *A. kochii*, *A. adnatum*, *Entodon cladorrhizans*, and *Mnium cuspidatum*. The tests for the mosses, bark, and soil ranged 7.2–7.6 except in one case where the moss and bark went to 6.8.

The third wood studied for tree mosses was a portion of the eastern part of the pine-oak mixture at The Pines. Part of the work was in a thick growth of oaks with a heavy undercover, part in open timber, and the rest in a thick group of young pines. The soil was sand and gravelly till of the Illinoian ground moraine, covered generally with a layer of humus. In the oaks *Psedera quinquefolia*, *Celastrus scandens*, *Galium* sp., and many other forms hid the ground except in spots. Under the pines needles made such a thick coating of humus that few other plants could get a start. On tree bases, old logs, and stumps among the oaks were found *Mnium cuspidatum* and *Amblystegium serpens*. These tested from 7.0 to 8.2 on soils testing from 4.8 to 7.0. In the young pines the mosses were confined to the bases of trees and barren soils. The prevailing species were *Brachythecium rutabulum*, *Amblystegium serpens*, *Amblystegiella adnatum*, *Bryum roseum*, and *Catharinea undulata*. Tree mosses tested from 6.8 to 7.6 and soil mosses ran between 5.4 and 6.4. The pH of the soil under these pines varied from 4.0 to 7.0. A few small clumps of *Dicranella heteromalla* at the base of the larger pines ran to 4.4 on soil with a pH of 4.2. In all cases where a moss was found both on tree base and soil the soil specimen tested more acid. One case of *A. adnatum* on the bark of a pine showed a reading of 5.4, which is unusually low for tree mosses. In general these tests showed that tree mosses of this region were from neutral to the limit of the alkaline scale. Individual tests in other plots corroborated these data (table IV).

Pine Woods

About 6 miles east of Polo, where the Burlington Railroad crosses Pine Creek, is the last important vestige of native white pines of north-

ern Illinois. At this point the creek has cut a valley 50–100 feet deep with vertical cliffs and steep slopes on the sides. The pines occupy a narrow strip along the east bluff for a distance of about 1 mile. Not only have the old pines been able to maintain themselves, but young trees are springing up among the oaks farther back, making good headway toward resetting other parts of the woods in pines. Mosses do not form a noticeable part of the pine wood flora; therefore the major effort of this study was spent along the bluffs of the valley.

TABLE IV

Species	Range of pH	
	Moss test	Test of soil 1 inch deep
Catharinea crispa	7.6	7.6
Catharinea angustata	5.4	.....
Catharinea undulata	5.6–6.4	.....
Dicranella heteromalla	4.2–7.0	4.4–6.8
Physcomitrium turbinatum	6.0	.....
Bryum roseum	6.2–7.6	.....
Mnium cuspidatum	7.4–8.2	7.4–8.2
Anomodon minor	7.6	.....
Anomodon rostratus	7.4–7.6	.....
Anomodon attenuatus	7.4–7.6	.....
Brachythecium oxycladon	7.6	.....
Brachythecium rutabulum	5.4–6.8	4.2–6.0
Amblystegium adnatum	7.2	7.2
Amblystegium serpens	7.2–8.2	5.2–8.2
Amblystegiella adnata	7.2	.....
Entodon cladorrhizans	7.4	.....
Entodon seductrix	7.0–7.2	.....

The bluffs are steep slopes covered with enough soil to support a good growth of oaks, elms, hop hornbeams, and cedars, with pines on the upper edge or they are vertical cliffs of solid limestone (Platteville) which carries a scant mixture of lichens, cliff brakes, mosses, and liverworts. The soil of this region is till from the Illinoian ground moraine. Along these bluffs it is a thin layer, but in many places it is covered with a mesophytic vegetation of *Claytonia virginica*, *Ranunculus septentrionalis*, *Arisaema triphyllum*, *Dentaria* sp., *Viola* sp., *Podophyllum peltatum*, and others of this type.

West Bluff

The west bluff comprises a large area, including a part of the bluff of the main stream, cliffs, banks, and other plots along a small tribu-

tary stream that cuts through it from the northwest. The mosses of this area are practically all soil and rock species. On the whole the habitat is dry and thinly covered with vegetation.

The portion of the bluff along the main stream is a precipitous slope with a south face. The soil is thin except at the base, where it supports a growth of walnuts and elms. At the top limestone outcrops are numerous, and the most common tree found here is the cedar. Under the cedars a few poor specimens of *Aquilegia canadensis* have been able to get a footing on the ledges. Lower, *Aquilegia*, *Thalictrum dioicum*, *Rubus occidentalis*, and *Viola cucullata* are representative species. The slope is well shaded and the sunlight reaches only small spots for short periods each day. During the wet seasons mosses grow vigorously but in the summer they are usually dormant. The common mosses are *Grimmia apocarpa*, *Amblystegium serpens*, and *Mnium cuspidatum*. The substratum is soil, rock, shallow soil, and decaying wood. They form thin mats only and do not add much to the humus layer. Because these mosses are growing so close to the limestone surface, all pH tests were alkaline, ranging 7.6–8.2. The correlation was very close, since the soil layer is usually the top material to which the mosses were attached.

Several rods west of this bluff a small tributary flows in from the northwest. It has cut a deep valley in the limestone, leaving rocky cliffs and soil banks on which many mosses have become established. On the rocky cliffs the cedars are the only trees that can grow, but in the valley and on the lower slopes walnuts, elms, hackberries, and oaks are common. Grasses, *Aquilegia*, *Galium* sp., *Ranunculus fascicularis*, *Cynoglossum officinale*, *Viola cucullata*, and dwarfed strawberries make up the ground flora. The substrata are limestone and disintegrated rock with alluvium in the valley.

The mosses growing on the ledges and surfaces of the rock exposures were *Brachythecium oxycladon*, *B. rutabulum*, *Anomodon rostratus*, *Grimmia apocarpa*, *Barbula unguiculata*, and *Mnium cuspidatum*. On account of the dry and hard conditions all mosses showed thin mats of scanty growth. The pH readings were all highly alkaline, 8.0 and 8.2, owing to the presence of limestone. In the valley *Bryum caespiticium* was the only moss that grew in abundance. It tested 8.0 as well as the soil. The soil mosses of the bluffs were *Bryum caespiticium*, *Brachythecium oxycladon*, *B. rutabulum*, *Catha-*

rinea undulata, and *Ceratodon purpureus*. Some of these grew in dense mats in the open spaces between the trees. These mosses ranged between 6.8 and 8.2 with the median on the alkaline side (table V). One group of mosses consisting of *Thuidium recognitum*, *Polytrichum juniperinum*, and *Catharinea angustata*, growing on a gravelly moraine tested from 5.2 to 5.8. The soil just below the mosses ran from 5.2 to 5.6. These mosses were well established and grew rapidly during the wet seasons. In this territory the mosses were closely confined to soils of their liking: the acid mosses held to acid soils and the alkaline species were found in their respective conditions.

TABLE V

WEST BLUFF AT PINE WOODS; TESTS OF MOSSES AND TOP SOIL

SPECIES	RANGE OF pH																
	5.0	5.2	5.4	5.6	5.8	6.0	6.2	6.4	6.6	6.8	7.0	7.2	7.4	7.6	7.8	8.0	8.2
Brachythecium oxycladon																	5
Brachythecium rutabulum													1				
Anomodon minor														1			
Anomodon rostratus																	1
Amblystegium serpens																	1
Grimmia apocarpa														1			2
Barbula unguiculata																	1
Bryum caespiticium																1	
Mnium cuspidatum															2	1	
Polytrichum juniperinum				1	1												
Catharinea angustata		1		1						2			1				
Ceratodon purpureus			1														
Thuidium recognitum				2	1												

EAST BLUFF

The east bluff has a long steep slope covered with a layer of glacial till and disintegrated rock. It has little rock exposure except in one small section where the limestone forms a vertical cliff. The whole bluff is mesophytic in character, even the rock cliff being moist enough in parts to support a growth of mosses and liverworts. The trees of this hillside consist of *Ulmus americana*, *Quercus alba*, *Q. rubra*, and *Ostrya virginiana*, with black walnut and red cedar at the base and the pines at the top. Since the ground vegetation is thick, the mosses find it difficult to become established. Small open

spaces, loose rocks, old logs, and tree bases are the spots on which they have been able to grow. The shade is dense and moss mats are usually small, thin, and not very vigorous.

The mosses growing in the edge of the pines at the top of the slope showed a different reaction from those farther down. They consisted of *Dicranella heteromalla* on soil at the base of pines, *Catharinea undulata*, *Ditrichum pallidum*, and a few specimens of *Mnium cuspidatum* and *Brachythecium rutabulum*. *Dicranella* was on soil that tested from 3.8 to 5.3, *Catharinea* ran between 6.2 and 7.4 on soil testing 5.3–6.0, and the other mosses ranged 6.0–6.8 while the soil varied around 5.8 and 6.0.

The reactions from a few yards below the top to the base were all from neutral to 8.0 in the alkaline scale. The mosses were chiefly pleurocarps consisting of *Brachythecium oxycladon*, *B. rutabulum*, *Amblystegium serpens*, *A. varium*, *Anomodon attenuatus*, *A. apiculatus*, *Pylaisia schimperi*, *Entodon cladorrhizans*, *Fissidens taxifolius*, and *Mnium cuspidatum*. *B. oxycladon*, *Mnium*, *Pylaisia*, *A. varium*, and *Entodon*, all growing on rotting wood and soil nearby, tested 5.6, 5.6, 5.2, and 6.8 respectively. All mosses found on soil or rock, including some of these, tested from 7.0 to 8.0. The soil tests were all within the upper one-half inch, and were included with the mosses. The acid soils at the top were characteristic of pinewoods, and the alkaline reactions on the lower slope were the usual type for a region of this kind. The most striking feature about this habitat so far as mosses are concerned was that the pleurocarp forms seemed to be better adapted to a shady, mesophytic, alkaline hillside such as this than the acrocarp forms.

A small section of the east bluff breaks into a vertical limestone cliff about 40 feet high. Three or four feet of glacial till cover the top edge, giving rooting for the large pines that grow close to the margin. Along a portion of the cliff there seems to be a seeping of water which runs down over the side, giving moisture to a thick coating of plants. These consist of *Conocephalus* (*Conocephalum conicum*), mosses, and such flowering plants as *Asarum canadense*, *Arisaema triphyllum*, *Hepatica triloba*, *Dicentra* sp., and *Mitella diphylla*.

The common mosses on the cliff and the talus at the foot are *Brachythecium oxycladon*, *Anomodon attenuatus*, *Mnium cuspidatum*,

and *Bryum roseum*. In places the mosses make a thick mat that covers the rock completely. The pH tests are all alkaline, 7.6 to 8.2 (table VI).

TABLE VI

Species	Range of pH	
	Moss tests	Test of soil 1 inch deep
Catharinea undulata	5.2–7.4	6.0–7.4
Dicranella heteromalla	3.8–4.6	3.8–4.6
Ditrichum pallidum	6.2–6.4	.....
Pottia truncata	6.4	.....
Physcomitrium turbinatum	6.8	.....
Mnium cuspidatum	5.2–8.0	5.6–8.0
Fissidens taxifolius	7.4	.....
Brachythecium oxycladon	5.6–8.0	5.6–7.4
Brachythecium rutabulum	7.0–8.0	7.0
Anomodon apiculatus	7.2	.....
Anomodon attenuatus	7.2–8.0	.....
Amblystegium varium	5.2–8.0	.....
Amblystegium serpens	7.4–8.0	.....
Plagiothecium turfaceum	7.2	.....
Entodon cladorrhizans	6.8	.....

Devil's Backbone

The Devil's Backbone is a prominent ridge of St. Peters sandstone about 2 miles south of Oregon. Back from the road a short distance the ridge is topped by Platteville limestone, but near the road this has eroded leaving the friable sandstone exposed. This is rough and broken, forming many shelves, crevices, and flats for the growth of plants. Such places are filled with sand and small amounts of humus left from plant débris. As is the case in most conditions of this type, the south slope is xerophytic and the north more nearly mesophytic. The talus on the south side is almost pure sand, but on the north it is covered with a layer of humus formed from fallen leaves and other forest materials. Above the talus on both sides the rock is precipitous. It was this part of the ridge that gave most of the data for this work. The common species able to maintain a foothold on these ledges are *Vaccinium vacillans*, *Amelanchier canadensis*, *Rumex acetosella*, and a few scattered grasses and sedges. On the north side, where there is more moisture and shade, *Polypodium vulgare* has found lodging in the crevices.

The mosses found on this hill are typical of this kind of place. *Polytrichum commune*, *P. piliferum*, *P. ohioense*, *Catharinea angus-*

tata, Ceratodon purpureus, Dicranum scoparium, Dicranella heteromalla, Leucobryum glaucum, Pohlia nutans, Bryum caespiticium, and *Plagiothecium pulchellum* have become established in various spots over the surface. On the south side they have formed mats on the thin sand covering the ledges. Growth is stunted and only a few plants produce any fruiting stalks. At the top of the highest part of the ridge the soil is so thin and the exposure so complete that *P. piliferum* alone has been able to maintain itself to any noticeable extent. It is mixed with *Cladonia sylvatica* and *C. pyxidata.* The mosses on

TABLE VII

DEVIL'S BACKBONE AND SINNISSIPPI KNOB; TESTS OF MOSSES AND TOP SOIL

SPECIES	RANGE OF pH																
	3.8	4.0	4.2	4.4	4.6	4.8	5.0	5.2	5.4	5.6	5.8	6.0	6.2	6.4	6.6	6.8	7.0
Polytrichum commune	...	...	1	4	2	1	...	2	1	2	1	...	1	1	...	...	...
Polytrichum piliferum	1	...	2	1	2	1	1	1	2	1	1	...	...	...	...	...	...
Polytrichum ohioense	...	1	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Catharinea angustata	...	...	...	...	1	...	1	...	3	3	...	...	...	...	...	...	...
Hedwigia albicans	...	...	...	...	...	...	...	2	1	...	...	...	1	...	...	...	...
Ceratodon purpureus	...	...	...	...	2	...	...	1	2	...	...	...	1	...	1	1	...
Dicranum scoparium	1	...	2	...	3	...	...	4	1	1	...	...	...	...	...	...	...
Ditrichum pallidum	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...
Dicranella heteromalla	1	...	2	...	...	1	...	3	1	...	...	...	...	...	...	...	...
Leucobryum glaucum	...	...	...	...	1	3	...	...	...	...	...	...	...	...	...	...	...
Bryum caespiticium	...	...	2	...	2	...	...	...	1	...	...	...	...	...	1	...	...
Pohlia nutans	1	1	1	1	5	...	1	...	2	2	1	...	...	...	...	...	...
Brachythecium rutabulum	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...
Calliergon schreberi	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...
Plagiothecium pulchellum	...	1	2	...	1	...	...	...	...	...	...	...	...	...	...	...	...

the north side are not any more numerous, but make a much more prolific growth than on other parts of the hill. They grow on ledges, in crevices, and on the vertical rock face without difficulty, and are able to fruit in season.

This hill was highly acid in all the places tested. The pH range for the mosses and the soil in their rhizoids was 3.8–5.4 (table VII). Readings of the sand not deeper than 1 inch ran 3.8–4.6. The adjustment of the moss flora on this rock was the closest found anywhere in the region. *Polytrichum ohioense* was found on the moist north slope. The other two species of *Polytrichum* were in drier places but in the same type of soil. *Plagiothecium pulchellum* grew well on the

acid rock in rather dry but shady spots. *Dicranella heteromalla*, *Dicranum scoparium*, and *Pohlia nutans* thrived on all sides but did best on the wetter face. Although the amount of water had much to do with the growth of the moss mat, it did not make much difference in the H-ion concentration of either the soils or the mosses.

Sinnissippi Knobs

A few rods south of the Devil's Backbone are two prominent Knobs. These are of St. Peter sandstone with low and well rounded tops. The slopes are gentle and support a moderate mesophytic plant cover. There are some barren rock exposures at the top, but the surface is broad and is covered with a thin layer of soil. Trees of the oak-hickory climax reach almost to the tops and give a medium shade on the east, north, and west sides. The best growth of mosses is on these three sides and the tops.

The bases of the east slopes of these two hills were much alike and had similar moss floras. The common mosses were *Ceratodon purpureus*, *Funaria hygrometrica*, *Bryum caespiticium*, *Brachythecium rutabulum*, and *Amblystegiella adnata*. The mosses gave pH readings from 5.2 to 6.6 while the soil tests ran 4.8–5.6. These forms were growing well but did not develop into large thick mats. From half way up to the tops the moss species changed noticeably. Approaching the summits *Dicranella heteromalla*, *Bryum caespiticium*, *Catharinea angustata*, *Polytrichum commune*, *Pohlia nutans*, *Hedwigia albicans*, *Entodon seductrix*, and *Calliergon schreberi* appeared in well developed plots. *Dicranum scoparium* and *P. piliferum* occupied the higher places at the top. The pH tests of this group showed higher acid conditions than near the bases. The range for the moss materials was between 4.2 and 6.4 and the soil ran 4.2–5.6. In one case *Entodon seductrix*, growing near the top on rock, tested 6.8 for both the moss and thin layer of soil, but in most of the tests the pH stood about 5.2 and 5.4.

While the H-ion concentration at the bases of the slope approached close to the neutral point, the upper parts of the hills showed the usual acid reactions for the sand exposures of the region. Again it may be noted that it made little difference regarding the moisture content of the substratum. Tests from moss plots on bare rock ran

much like those on the sand and humus soil which held more moisture.

In the surrounding woods were many excellent moss plots. Growing on the rocks and sand were *Polytrichum commune*, *P. piliferum*, *Hedwigia albicans*, *Dicranum scoparium*, *Ditrichum pallidum*, *Ceratodon purpureus*, and a few other scattered species. Although the plots were not large, growth was good and sporophytes were usually present. The pH range of the moss material was 5.2–6.8 and that of the soil 4.4–5.6. A few tree mosses gave a different reaction. They consisted of *Pylaisia schimperi*, *Brachythecium rutabulum*, *Amblystegiella adnata*, and *Anomodon attenuatus*. Tests of this group ran between 5.6 and 7.4 with the majority between 6.8 and 7.2. Although these were miscellaneous spots, the mosses occupying the different places were very true to type.

Castle Rock and vicinity

No other spot along the Black Hawk trail is more widely known and more frequently visited than the sandstone prominence about 3 miles south of Oregon called Castle Rock. It stands 100 feet or more above the river. The top is hard sandstone but the base on three sides is well built up from eroded sand which gives a good place for the growth of plants. The north side, being better shaded, supports some excellent beds of mosses. Characteristic plants of this slope are *Quercus alba*, *Q. ellipsoidalis*, *Amelanchier canadensis*, *Rubus allegheniensis*, *Vaccinium vacillans*, *Maianthemum canadense*, *Polygonatum biflorum*, *Smilacina racemosa*, and *Dicentra cucullaria*.

In the vicinity of Castle Rock are five other hillsides upon which are found excellent moss plots. Three of them are south slopes and the other two are north. All are St. Peter sandstone outcrops, usually supporting the mesophytic vegetation commonly found in the oak woods of this region. The substrata are of sandy soil, generally mixed with humus of various depths, none exceeding 4 inches, and rock faces that are kept moist throughout most of the year by precipitation and seepage. All these places are well shaded during the growing season, either on account of the position of the hillside or by trees.

Mosses grew in great profusion in these several places. They occu-

pied rock ledges, shallow caves, vertical faces, moist and arid spots, and places of both shade and open sunlight. In many places they grew in such dense mats that they not only added humus to the soil but prevented erosion of the loose sand. The heaviest mats were of *Polytrichum commune*, *P. piliferum*, *Dicranum scoparium*, *Dicranella heteromalla*, *Catharinea angustata*, and *Calliergon schreberi*. In one place dead stems of *P. commune* extended more than 4 inches below the present level of the soil.

The mosses commonly found in this region are *Polytrichum commune*, *P. piliferum*, *Catharinea angustata*, *Dicranum scoparium*, *Ditrichum pallidum*, *Dicranella heteromalla*, *Pohlia nutans*, *Funaria hygrometrica*, *Georgia pellucida*, *Ceratodon purpureus*, *Amblystegiella adnata*, *Calliergon schreberi*, *Brachythecium rutabulum*, and *Mnium cuspidatum*. Others occurred less frequently and seemed to be out of their range, such as *Brachythecium oxycladon*, *Plagiothecium denticulatum*, *Anomodon attenuatus*, and *Bartramia pomiformis*. Even though the latter group was out of its natural habitat, the individual species maintained their usual reactions about the neutral point, 6.6–7.4. *P. commune* growing among these mosses also tested as high as 6.8.

The H-ion concentration of this whole group of moss habitats is consistently high, scarcely going below 5.6 in the soil tests at the 1 inch level. In a few cases the top soil with humus and rhizoids ran to 6.4–6.6. The pH readings for the mosses correlated closely with those of the soils, ranging from 4.2 to 6.8 (table VIII). This correlation, together with the fact that the mosses grew so vigorously and produced sporophytes, indicated strongly that so far as the moss flora of this region was concerned it was a climax situation. The few neutral and alkaline species found were not showing the vigor and growth noticed in the other group. Their present condition suggested that they were probably remnants of an earlier moss flora of a different type.

Species range

The preceding observations give some idea of the H-ion concentration of each of the different areas tested, but in no case were enough tests made of the individual species to be more than suggestive. The number of tests ranged from one for several species to

96 for *Polytrichum commune*. There was no special effort to favor any particular moss, but the number of tests indicates in a good measure the relative importance of each one in the Grand de Tour region. In this respect *P. commune* stands far above the rest, having occurred in every area where there was a sandy soil base.

Consideration of the species range requires a great number of pH readings to reach any definite conclusions. Since this work was not directed specially toward that problem, but to a more general pur-

TABLE VIII

Species	Range of pH	
	Moss tests	Tests of soil below surface
Polytrichum commune	4.2–6.8	3.8–6.4
Polytrichum piliferum	4.4–6.8	4.2–6.8
Catharinea undulata	6.6	4.6
Catharinea angustata	4.4–6.2	3.8–5.4
Georgia pellucida	3.8–5.6	4.2–5.2
Ceratodon purpureus	4.8–6.4	4.4–5.8
Dicranum scoparium	4.0–5.6	4.0–6.4
Ditrichum pallidum	4.4	4.2
Ditrichum tortile	4.2	.....
Dicranella heteromalla	4.4–7.0	3.8–6.0
Pohlia nutans	3.8–5.2	3.8–5.0
Bryum caespiticium	4.8–6.8	5.4
Mnium cuspidatum	5.0–5.8	.....
Anomodon rostratus	7.4	4.6
Anomodon attenuatus	6.2–7.0	5.2
Brachythecium oxycladon	6.4–6.8	4.4–5.2
Brachythecium rutabulum	7.0–7.2	5.2
Amblystegiella adnata	4.6–4.8	.....
Calliergon schreberi	4.8–7.2	4.2–7.4
Plagiothecium denticulatum	4.8–5.8	4.2–5.4
Hypnum haldanianum	4.0–5.0	4.0

pose, it is not expected that these figures should be considered final. Altogether there were 62 species of mosses found in this territory, belonging to 14 different families. Of these only 20 species showed tests of 10 or more, while 9 had 20 or more. A few of the outstanding ones will be mentioned merely for the purpose of emphasis.

All species of *Polytrichum* were acid and grew on acid soils. *Catharinea undulata* preferred soil from neutral to low acid, while the moss and top soil materials ranged from 5.4 to 8.2 with the majority of tests about neutral. *C. angustata* on the other hand was found in more acid soil and had a higher H-ion concentration than its related

species. *Pohlia nutans*, *Dicranum scoparium*, and *Dicranella heteromalla* also grew well in acid soils. Two pleurocarps showed a preference for acid soils, *Calliergon schreberi* and *Hypnum haldanianium*. The outstanding mosses that ran from about the neutral point to the alkaline end of the scale were *Mnium cuspidatum*, *Bartramia pomiformis*, *Aulacomnium heterostichum*, *Brachythecium* spp., *Anomodon* spp., *Thuidium recognitum*, and *Climacium americanum*. *Ceratodon*

TABLE IX

RANGE OF pH OF MORE COMMON SPECIES FOUND IN REGION

SPECIES	RANGE OF pH																														
	3.8	4.0	4.2	4.4	4.6	4.8	5.0	5.2	5.4	5.6	5.8	6.0	6.2	6.4	6.6	6.8	7.0	7.2	7.4	7.6	7.8	8.0	8.2
Polytrichum commune	...	...	1	2	5	3	10	14	8	11	3	4	5	5	6	11	1	1	3	1	...	...	...
Polytrichum piliferum	...	...	2	...	3	2	2	6	7	6	1	...	2	...	...	3	...	1	...	...	...	...	...
Catharinea undulata	...	1	...	...	...	...	...	...	1	1	...	2	3	5	5	2	6	5	4	5	...	...	...
Catharinea angustata	...	...	...	1	1	1	4	6	6	6	...	3	2	3	1	2	...	...	1	1	...	...	...
Dicranum scoparium	1	1	2	1	2	...	1	10	4	5	...	1	...	...	1	...	...	...	...	...	...	...	...
Dicranella heteromalla	2	...	2	4	1	1	...	3	3	1	...	...	...	1	...	...	1	...	...	...	...	...	...
Pohlia nutans	1	1	3	3	6	3	2	11	4	4	2	1	...	...	...	...	...	...	...	...	...	...	...
Ceratodon purpureus	...	...	...	...	4	1	...	1	3	...	...	...	2	1	1	1	...	...	3	1	...	...	...
Georgia pellucida	1	...	2	1	1	2	2	2	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Bryum caespiticium	...	...	2	...	2	1	1	2	...	...	...	...	...	...	1	...	2	...	...	1	...	...	...
Bartramia pomiformis	...	...	...	...	...	...	...	1	...	...	2	...	1	...	1	1	5	10	3	3	4	...	...
Aulacomnium heterostichum	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	2	1	5	3	4	1	...	...
Mnium cuspidatum	...	...	...	...	...	1	1	2	1	1	2	1	...	2	2	1	1	9	9	4	3	2	2
Thuidium recognitum	...	...	...	...	...	...	...	1	...	2	2	2	...	...	3	1	...	2	2	1	...	...	...
Brachythecium oxycladon	...	...	...	...	1	...	...	...	...	...	...	1	...	...	...	...	1	1	3	2	...	2	2
Brachythecium rutabulum	...	...	...	...	1	...	...	...	1	1	1	...	1	4	1	2	1	2	4	1	3	3	...
Calliergon schreberi	...	...	...	...	...	...	1	...	...	2	1	1	...	...	...	4	...	...	...	...	...	...	...

purpureus although found on acid soils had a rather well distributed range, 4.6–7.6.

Another significant fact shown by these data was that the soil on which the mosses grew usually tested a little higher acid than the moss materials and top soils. The soils were not more constant at the 0.5–1 inch depth than the mosses, but seemed to vary rather closely with them. These two points seemed to be suggested, namely, the more acid the moss the more acid can be the soil on which it may grow; and the more alkaline the moss the less acid the soil which it will tolerate. Table IX gives the pH range for the mosses

that occurred most frequently. A list of mosses occurring in the region so few times that they were not charted is given in table X.

TABLE X

Moss	Number of tests	pH range	Moss	Number of tests	pH range
Polytrichum ohioense	3	4.0–4.2	Anomodon minor	1	7.4
Polytrichum juniperinum	2	5.6–5.8	Anomodon attenuatus	12	6.8–8.2
Catharinea crispa	1	7.6	Anomodon rostratus	5	7.4–7.8
Fissidens taxifolius	1	7.4	Anomodon apiculatus	1	7.0
Fissidens adiantoides	1	7.0	Thelia lescurii	2	7.0–7.2
Ditrichum pallidum	5	4.8–6.4	Leskia gracilescens	1	7.6
Dicranum flagellare	1	4.6	Hylocomium triquetrum	3	6.6–7.2
Dicranum pallidum	3	5.0–5.2	Eurhynchium hians	1	7.6
Leucobryum glaucum	4	4.6–5.0	Eurhynchium serrulatum	12	7.0–8.2
Grimmia apocarpa	4	7.4–8.2	Brachythecium salebrosum	3	5.4–7.0
Hedwigia albicans	5	5.4–6.2	Amblystegium serpens	10	5.8–8.2
Tortula ruralis	1	7.8	Amblystegium varium	12	5.2–8.2
Barbula unguiculata	2	7.4–8.2	Amblystegium adnatum	2	7.2
Encalypta ciliata	2	7.6	Climacium americanum	8	6.6–7.8
Funaria hygrometrica	2	5.2–7.6	Hypnum haldanianum	5	3.8–5.4
Physcomitrium turbinatum	2	6.0–6.6	Plagiothecium pulchellum	4	4.0–6.0
Timmia cucullata	4	8.2	Plagiothecium turfaceum	3	7.4
Bryum argenteum	4	6.2–8.2	Plagiothecium denticulatum	4	4.8–6.8
Bryum roseum	3	6.2–7.6	Amblystegiella adnata	7	4.6–7.2
Bryum binum	3	4.8–5.0	Entodon seductrix	7	6.8–7.6
Mnium hornum	2	7.0–7.4	Entodon cladorrhizans	3	6.8–7.4
Mnium stellare	6	5.8–8.2	Pylaisia schimperi	5	5.6–7.4
Mnium spinulosum	2	6.4–7.0			

Summary and conclusions

1. Mosses seem to have an H-ion range within which they can grow. Within these limits the optimum is usually near the median.

2. Mosses on the sandy soils of this region are generally the acid-loving types, although some are alkaline.

3. On the hilltops and on sandstone the mosses are acid-loving; at the bases of the hills and on the sides they may be alkaline.

4. Tree mosses run from neutral to alkaline; those on old wood are acid.

5. Mosses on limestone and the thin soils overlying it are alkaline; those on the banks of the small streams are also alkaline.

6. Most acid-loving mosses are acrocarps; most alkaline mosses are pleurocarps.

7. There is a close correlation of pH between the mosses and the substratum on which they are attached; there is some correlation between the mosses and the deeper soil, but not so close as with the former.

8. Moisture supply is an important factor in moss growth even when the H-ion concentration is suitable.

9. Mosses in mixed groups have a similar pH adjustment.

10. There are some indications that the mosses in this region have followed in successions.

11. Soil tests conform to the usual type. Hilltops and upper flats are acid while lower slopes and bases are neutral to alkaline.

12. Mosses have adjusted themselves to these conditions rather closely. They seem to have the same general relations to their substratum, so far as H-ion concentration is concerned, as the plants of the higher orders.

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ANTHERIDIAL DEHISCENCE IN THE POLYPODIACEAE

M. ELIZABETH HARTMAN

(WITH TWENTY-SEVEN FIGURES)

Introduction

Antheridial dehiscence in ferns has been under consideration since NÄGELI (**23**) in 1844 discovered the true antheridia. Various points of view concerning the dehiscence have been advanced, and taxonomic significance has been assigned to it. Separation of the Cyatheaceae and the Polypodiaceae partially on the basis of method of antheridial dehiscence is a striking example. In the Cyatheaceae the opercular cell was known to be extruded; in the Polypodiaceae it was believed to be ruptured. In 1911, however, SCHLUMBERGER (**28**) declared this distinction invalid, for he found extrusion of the cover cell to be characteristic of members of both families. His work, although accepted by GOEBEL (**13**), was not wholly accepted by English and American investigators. Further investigation of antheridial dehiscence in the Polypodiaceae was considered desirable, therefore, and these studies were begun in 1925. The morphological aspect of the problem was first considered and investigation of living material made. Microchemical studies were later attempted, in an effort to explain more fully the mechanism of dehiscence. These two phases will be treated separately. The following historical summary indicates the present status of the problem.

Materials and methods

The general method employed in this investigation was direct microscopic observation of living material mounted in distilled water; in addition, a few prepared slides were made. The photomicrographs were made with a Bausch and Lomb apparatus from living specimens, and a camera lucida was employed in drawing. For most of the work a no. 10 ocular and 4 mm. objective were used.

The cultures were grown in covered glass vessels kept on a laboratory table by a north window, with the same side of the dish always

HISTORICAL SUMMARY

DATE	INVESTIGATOR	MATERIAL	INTERPRETATION OF DEHISCENCE
1844	Nägeli (23)	Over 100 species from botanical garden at Zürich, grown for germination studies; figures Aspidium augescens, A. concinnum, Asplenium dissectum	Antheridium splits at summit. Whether mature or not, if brought into contact with water it discharges contents.
1848	Leszczyc-Suminski (20)	Various species, particularly Pteris serrulata	Spontaneous apical rupture at maturity.
1849	Wigand (37)	Various species growing on flower pots, including Adiantum pubescens, A. capillus-veneris (?), Pteris sp., Aspidium capense, etc.	Star-shaped apical rupture through pressure or spontaneously at maturity. Agency of water seems unessential.
1849	Thuret (32)	Various species; figures Scolopendrium officinale and Pteris aquilina	Apical cell ruptured or sometimes discharged through hole in "cuticle" by pressure of enlarging spermatogenous mass; process comparable with that in mosses. Subsequent intrusion of ring cell.
1849	Schacht (27)	Pteris serrulata, Asplenium petrarcae, Adiantum formosum, Aspidium violaceum	Cover cell gradually lifts itself more or less completely from other cells, but also frequently seems to burst. State of ripeness, rather than presence of water, apparently essential factor.
1862	Hofmeister (17)	General; figures Pteris serrulata for antheridia	If ripe antheridium brought into contact with moisture, its contents swell and apical cell bursts in stellate manner.
1869–1870	Strasburger (29)	Pteris serrulata (and Ceratopteris thalictroides)	Star-shaped rupture of cap cell results from pressure of interior, if ripe antheridium brought into contact with water.
1869	Kny (19)	Asplenium alatum, also non-polypod species including Cibotium schiedei	Cap cell at maturity irregularly ruptured, probably through turgescence of ring and basal cells. Folds in ring cell noted (cap cell detached in Cibotium schiedei).
1878	Bauke (2)	Pteris aquilina, P. cretica, cyatheoid species	Irregular rupture of cover cell in Polypodiaceae due to tension of peripheral cells and swelling of spermatogenous mass. Water important. Extrusion of cap cell characteristic in Cyatheaceae.

HISTORICAL SUMMARY—*Continued*

DATE	INVESTIGATOR	MATERIAL	INTERPRETATION OF DEHISCENCE
1896	Heim (16)	Doodia caudata, etc.	Undivided cap cell irregularly ruptured at maturity in Polypodiaceae through turgescence of ring cells.
1898–1901	Goebel (12)	General	Rupture of cover cells characteristic of the Polypodiaceae, Aneimia, and Mohria; details of mechanism unknown.
1902	Britton and Taylor (5)	Vittaria lineata	Cap cell ruptured centrally or laterally.
1908	Conard (9)	Dicksonia punctilobula	Cap cell ruptured irregularly; contents of antheridium swell by absorption of water.
1911	Schlumberger (28)	Cibotium schiedei, Hemitelia aspera, Cyathea dealbata, Diacalpe aspidioides, Woodsia obtusa, W. ilvensis, W. hyperborea, Cystopteris fragilis, Athyrium filix-femina, Asplenium ruta muraria, Scolopendrium officinale, Pteris serrulata, Polypodium aureum	Normal method of opening for polypod antheridium is detachment of cap cell; rupture absent. Water essential and wall cells take active part in opening.
1918	Campbell (7)	General; Onoclea struthiopteris used as type	Cap cell ruptured or less commonly extruded.
1918	Goebel (13)	General (follows Schlumberger)	Wall cells active in opening of antheridium in pteridophytes, as in bryophytes. Within the pteridophytes antheridia differ as to number of cells of apical layer taking direct part in opening. Detachment of one opercular cell is regular in leptosporangiates (including Polypodiaceae).
1921	Strasburger (30) (and others)	General	Cap cell ruptured by pressure of swollen ring cells. (This edition of textbook makes use of Schlumberger's figures of extruded cap cell.)
1923	Bower (3)	Leptosporangiate ferns in general	Cites Campbell, Goebel (1918), and Schlumberger. Uses figures of Schlumberger.
1927	Pickett and Thayer (24)	Polypodium vulgare var. occidentale, Pellaea densa	Antheridia open by pore which is 4-sided in Pellaea densa.
1928	Bower (4)	Dryopteroid ferns	Further reference to Schlumberger's work.

toward the light. At Mount Holyoke the substratum used was peat; in Nebraska, sphagnum. For most of the cultures the dishes and substrata were boiled in water. This process was found preferable to sterilization in the autoclave. When dry, the cultures were watered with distilled water. A number of the cultures survived the summer vacation seasons with very little care. Forceps dipped in 95 per cent alcohol and flamed were used in lifting the gametophytes.

Potassium permanganate was used, as necessary, to check the growth of molds. This treatment, suggested by Dr. STOKEY, proved effective. A few small crystals of the permanganate were added to distilled water in a dropper bottle, and a small quantity of the deeply colored solution ("decidedly pink" or even purple) dropped upon the infected areas, the treatment being repeated as often as seemed necessary. Care was exercised to avoid an excess of water in the cultures.

Both fresh and dried spores of native and greenhouse species were planted as available, a total of 24 species being cultured. Lack of time prevented the study of some of the cultures. The spores of *Microlepia platyphylla* (later identified by Dr. W. R. MAXON) were brought by Dr. STOKEY from Allan Park, Toronto.

Morphological investigation

In the preliminary studies, which consisted of observations of the frequency of cap cell extrusion in the available polypod species, the results varied from those with antheridia of *Microlepia platyphylla* (fig. 1), where a detached cap cell could be found for nearly every freshly opened antheridium, to those of the related species *Davallia pentaphylla*, where the detached cap cell was never seen during this early work. The fate of the cap cell, when it was not visibly extruded, remained undetermined. Neither the theory of a slightly tilted, lidlike cap cell under which the sperm mother cells might pass (SCHLUMBERGER **28**), nor the recognition of possible errors of observation seemed satisfactorily to account for the numerous failures to see the extruded cell.

The general conclusions from this unpublished work (1925) follow:

1. An extrusion of the cap cell, or its tilting, is indicated as the regular means of dehiscence for *Microlepia platyphylla*, *Dennstaedtia punctilobula* (both wild and pure), and *Aspidium marginale*.

2. An extrusion of the cap cell occurs also in *Polystichum acrostichoides* and *Woodsia ilvensis*.

3. It is probable that it may also be found in a wild hairy form, possibly *A. spinulosum*, and *Davallia pentaphylla*.

4. A rupture of the cap cell was never observed, although this alternative was not wholly disproved.

The morphological work was later continued (1926–1928) with more detailed study of the mechanism involved in the dehiscence, and increased effort to explain the instances when the detached cap cell failed to appear. Microchemical studies were also undertaken.

The changes in the ripe antheridium antecedent to opening were studied in greater detail, using greenhouse prothallia, probably *Aspidium simulatum*. Ripe antheridia were watched closely, the time period varying from a few minutes to three hours for an antheridium to open. The details observed were essentially those reported by earlier writers, including SCHLUMBERGER:

1. Gradual swelling of the spermatogenous mass.
2. Resulting compression of the peripheral cells: (a) imprint of the sperm mother cells first evident on the ring and cap cell and later on the funnel cell; (b) cap and ring cells sometimes scarcely perceptible; (c) funnel cell less completely compressed (this cell also differs from the others in stained sections, appearing redder with Flemming's triple stain).
3. Final opening instantaneous.
4. Quick inward protrusion of the previously distended peripheral cells, forcing out the sperm mother cells.
5. First ejectments very rapid.
6. Successive ejectments slower.

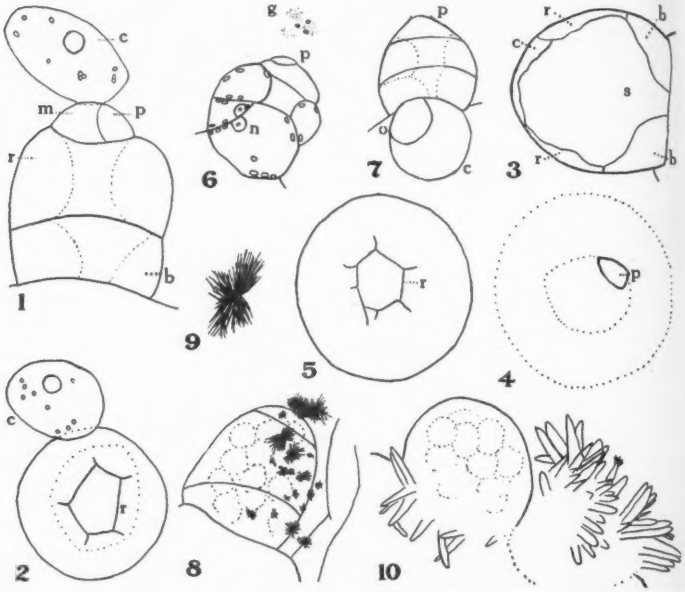
This process, with minor variations, seemed to characterize all species studied. As the swelling of the spermatogenous mass results in almost complete compression of the ring and cap cells and less compression of the basal cell, pressure of the swelling central mass together with that of the basal cell seems to be the primary agency in effecting the opening, while counter pressure of the ring and cap

cell seems to be secondary. A jerk immediately preceding dehiscence was noted with antheridia of *Polypodium iroides*, and was found to be a common accompaniment of the opening in various species. The compression of the peripheral cells before opening, in contrast with their expansion after, is illustrated in figs. 1–27.

Observations of the frequency of cap cell detachment were continued with variable results. Detached cap cells were now found for *Davallia pentaphylla*. With *Polypodium aureum*, however, actual extrusion was not observed. Sometimes this cell seemed to be in position, but tilted so as to permit the passage of the sperm mother cells. At other times, when a rupture seemed not improbable, folds in the ring cell were found to be responsible for the semblance of a star-shaped cleft, as explained by SCHLUMBERGER (figs. 2, 4, 5, 26). With *Aspidium marginale* detached cap cells frequently appeared. Antheridia of gametophytes from the drier situations in the culture vessels seemed to exhibit especially vigorous opening. Extrusion of the intact cap cell was occasionally observed with antheridia of *Woodwardia orientalis*. Tilted, lidlike cap cells were observed in *Adiantum pedatum;* many detached cap cells were observed in *Aspidium simulatum*, being seen readily even with low magnification. Detached opercular cells were also seen in *Polystichum acrostichoides*. Gametophytes of *Pellaea atropurpurea* showed opening antheridia, but no conclusive information concerning the dehiscence was obtained. In spite of this variability of results, there was no definite evidence of essential difference in antheridial dehiscence in the various species.

A study of the antheridia of *Adiantum pedatum* suggested the frailty of the detached cap cell as a factor in accounting for failures to see this cell after dehiscence. The detached cells seemed to disintegrate readily. In subsequent study of *Woodsia ilvensis* an extruded cell of very indistinct outline was seen. The dimness might have prevented its identification if the actual ejectment had not been observed. Two extruded cap cells of *Woodsia ilvensis*, however, observed later, seemed less evanescent. Of these, one was from the first antheridium to open in a group of twelve, simultaneously visible. Eight of the remaining eleven antheridia opened. They showed no detached cap cells after dehiscence, but only green granular mat-

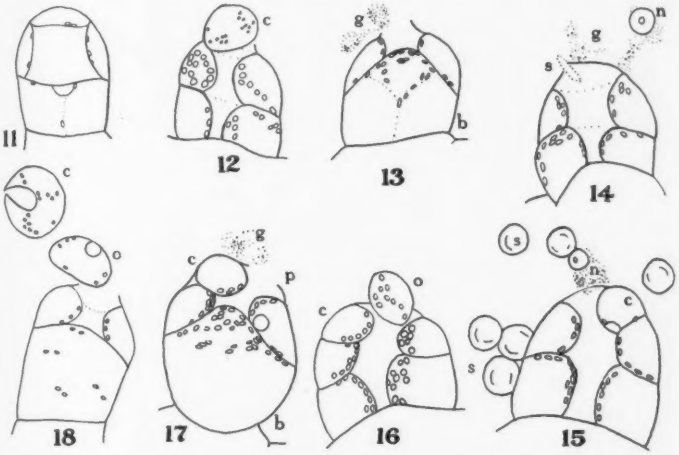
ter at the apex. Because of the frequency of the appearance of this granular material at the apex of open antheridia which failed to show the detached opercular cell, and of the similarity of its green granules to those seen in some of the detached cells, it seemed not



FIGS. 1–10.—Fig. 1, open antheridium of *Microlepia platyphylla*, lateral view; detached cap cell (*c*) showing nucleus and chloroplasts; outer membrane (*m*); pore in outer membrane (*p*); ring cell (*r*); basal cell (*b*); ×493. Fig. 2, *Adiantum pedatum*, apical view of antheridium; cap cell (*c*) folds in ring cell; ×333. Fig. 3, mature unopened antheridium of *Onoclea sensibilis*, optical section; spermatogenous mass (*s*); ×414. Fig. 4, *O. sensibilis*, apical view; pore in outer membrane (*p*); inner and outer edge of ring cell indicated with dotted lines; ×414. Fig. 5, same as fig. 4, lower level, showing folds in ring cell; ×414. Fig. 6, antheridium of *O. sensibilis;* pore in outer membrane (*p*); extruded granular mass (*g*); two nuclei of divided basal cell (*n*); ×293. Fig. 7, adjacent antheridia of *Athyrium filix-foemina* showing diagrammatic lateral view of normal antheridium with cap cell slightly projecting (*p*) and apical view of antheridium with division of original cap cell; opercular daughter cell (*o*); lunate daughter cell (*c*); ×414. Fig. 8, antheridium of *O. sensibilis* with glucosazone clusters on and near antheridium; ×414. Fig. 9, same as fig. 8; larger glucosazone cluster from field; ×414. Fig. 10, maltosazones massed about two antheridia of *O sensibilis;* antheridium on right almost covered by crystals; ×414.

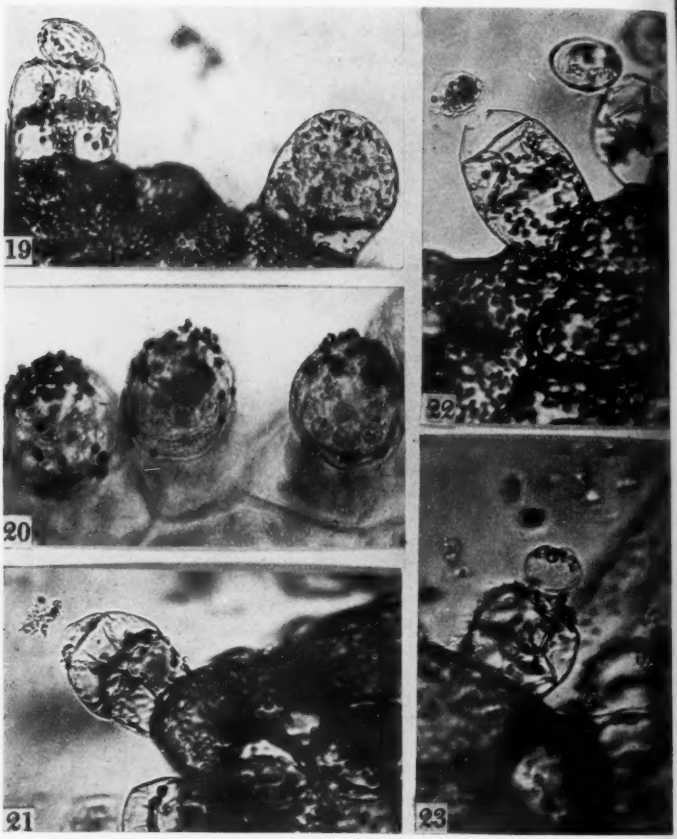
improbable that the green slime resulted from disintegration of the cap cell before or after dehiscence.

The occasional frailty of the cap cell was also observed with *Onoclea sensibilis*. At first detached cells were found with difficulty.

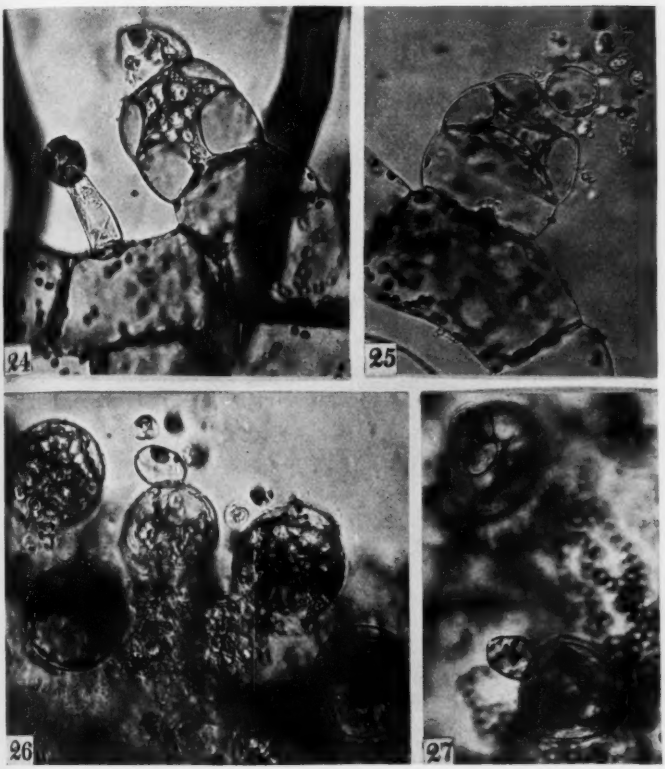


FIGS. 11–18.—*Woodsia obtusa:* Fig. 11, young antheridium. Fig. 12, antheridium with undivided cap cell partially extruded; pore in outer membrane visible. Fig. 13, antheridium with extruded content of undivided cap cell (pore in outer membrane evident, note swollen basal cell). Fig. 14, antheridium with extruded cap cell content containing nucleus with nucleolus; dotted ellipse represents elongated sperm mother cell (*s*) passing through pore in outer membrane. Fig. 15, antheridium with extruded content of opercular daughter cell, including nucleus, lunate daughter cell in place, and spermatocytes (*s*). Fig. 16, antheridium with divided cap cell; opercular daughter cell partially extruded; lunate daughter cell in position. Fig. 17, antheridium with extruded content of opercular daughter cell (nucleus in ring cell). Fig. 18, antheridium with divided cap cell; both daughter cells extruded (*o*, *c*) (nucleus visible in smaller daughter cell); ×293.

One became evident after the mass of sperm mother cells had scattered from the mouth of an antheridium. This cell, also, seemed evanescent: after 15 minutes it was too indistinct for identification, had its position been unknown. The wall seemed to dissolve in water. Numerous additional detached cells were found, some of which were in good condition 15 hours after extrusion. Most of these



FIGS. 19–23.—Fig. 19, *Onoclea sensibilis* showing open antheridium with tilted cap cell under which sperm mother cells passed (left) and mature unopened antheridium at right (note compression of wall cells before dehiscence and expansion after dehiscence). Fig. 20, *O. sensibilis;* antheridia from sugar test (Flückiger's) with crystals of cuprous oxide especially abundant at apex. Fig. 21, *Athyrium filix-foemina;* lateral view of open antheridium with extruded granular mass of cap cell content. Fig. 22, *A. filix-foemina*, showing opened antheridium with pore in outer membrane and detached cap cell with partially disintegrated content (right), and another detached cap cell. Fig. 23, *A. filix-foemina;* antheridium with detached cap cell showing nucleus; sperms and rhizoid visible in field; ×350.



FIGS. 24–27.—Fig. 24, *Woodsia obtusa;* open antheridium with undivided cap cell (out of focus and appearing as shadow); sperms within antheridium; glandular hair at left of antheridium; rhizoid as long shadow at right. Fig. 25, *W. obtusa;* filamentous thallus showing open antheridium with divided cap cell; opercular daughter cell detached; its sister cell in place; sperms about antheridium (cf. fig. 16). Fig. 26, *A. filix-foemina;* apical view of open antheridium with detached cap cell; unopened antheridia; old opened antheridium showing darkened cavity surrounded by folded ring cell; sperms in field. Fig. 27, *Alsophila cooperi;* (below) apical view of antheridium with divided cap cell, opercular cell extruded; (above) apical view of another antheridium with detached cap cell; ×350.

showed well defined wall, nucleus, and chloroplasts, although a few seemed to contain only small green granules (sometimes in active Brownian movement), and one or two, lying against the green thallus, were so indistinct that it is questionable whether an intact extruded cap cell or merely the green slime was seen. With lateral views of the antheridium the hole in the outer membrane was visible (figs. 1, 6, 12–14, 17–19, 22); with apical views the folds in the ring cell were conspicuous and the pore in the outer membrane could be seen at a higher level (figs. 4, 5). A striking example of the extrusion of the sperm mother cells under a tilted cap was also seen. The first sperm mother cells passed out under the cap cell (fig. 19), but successive ejectments gradually loosened it until it became wholly extruded. At other times all the exits were made under a tilted cap cell (figs. 7 *p*, 19); in some cases this cell was seen to be lifted by each escaping sperm mother cell and then to slip into position again. With *Cyrtomium falcatum* similar types of dehiscence were found, and also a resistant cap cell which withstood 10 minutes of heating on the water bath with acidified phloroglucinol.

Variability in the number of peripheral cells is a new feature found in antheridia of *Athyrium filix-foemina*. About 12 antheridia, each with a divided cap cell, were seen (fig. 7 *o*, *c*), and several antheridia with two ring cells in addition to the basal cell. Cap cell detachment was especially frequent and typical.

The occasional division of the cap cell in *Athyrium filix-foemina* is of interest. Both SCHLUMBERGER (28) and GOEBEL (13) state that it regularly remains undivided in the Polypodiaceae, and BOWER (4) records this opinion. Of the polypod genera previously investigated, only *Diacalpe* and *Woodsia* showed division. In *D. aspidioides* this division (according to SCHLUMBERGER) is strictly of the cyatheoid type, being accomplished by a transverse curved wall, sometimes followed by a second wall perpendicular to the first. In *W. obtusa* the division differs in that a definitely circular daughter cell is formed to one side of the original cap cell, and no further divisions occur. As division is frequent in *W. obtusa* and rare in *W. ilvensis*, this genus has been regarded as transitional between the Cyatheaceae and the Polypodiaceae.

In this study of the polypod antheridium, the division of the cap

cell was noted in *Woodsia obtusa* and *Athyrium filix-foemina*. These observations (figs. 7, 15–18, 25) may be compared with the cyatheoid type of division, as illustrated by *Alsophila cooperi* in fig. 27. In this connection it is of interest to note that both CHRISTENSEN (**8**) and WETTSTEIN (**36**) place the Woodsieae next to the Cyatheaceae.

Detailed study of *Woodsia obtusa* followed. Although both divided and undivided cap cells were found, the smaller daughter cell was often not evident before dehiscence because of its position and the compression due to the swelling of the spermatogenous mass. When the cap cell was divided, each daughter cell had a nucleus. In case of the undivided cap cell, the intact detached cap was sometimes found (figs. 12 *c*, 24) as in other species. When there were two cap cells, the smaller daughter cell was frequently extruded (figs. 16 *o*, 25). In one case both daughter cells were extruded, for two detached cells (one lunate and one ovoid) appeared before one open antheridium (fig. 18 *c*, *o*). Some open antheridia failed to show detached cells, but instead granular material appeared at the apex (figs. 13, 17). This slime, like that of other species, contained small green granules suggestive of the decomposing chloroplasts of the extruded cap cell.

The actual relation of this granular material to the cap cell seemed to be established when a nucleus with nucleolus was observed lying in the green slime (fig. 14 *n*). A second nucleus was seen in the material from another antheridium (fig. 15 *n*), this having a divided cap cell. Later nuclei were observed definitely in the extruded granular mass of other species, one from an antheridium of *Onoclea sensibilis*, and a few from antheridia of *Athyrium filix-foemina*.

Further to verify the idea that the green granular material is probably the content of the cap cell, additional antheridia were studied. With one antheridium of *Woodsia obtusa* it was definitely seen that the greenish granular slime preceded the spermatogenous mass. With *Cyrtomium falcatum* this priority of appearance was more readily observed, as the dehiscence is less nearly instantaneous. *Woodwardia angustifolia* also showed material appearing before the sperm mother cells, as does the detached cap cell. The hole in the outer membrane was seen distinctly.

The fact that the nucleus is not always seen with the green granules needs explanation, but does not necessarily discredit the theory

that these granules represent cap cell content. The nucleus may possibly disintegrate, as some of the observations seemed to show, or it may be hidden by the green granules. Being uncolored, it is frequently indistinct. A comparison of its visibility in extruded cap cells seemed significant. Of two detached cells lying side by side in *Athyrium filix-foemina*, one showed clearly defined wall, chloroplasts, and nucleus; the other less distinct wall and scattered green granules without well defined chloroplasts or nucleus. Of six detached cap cells from six successive marginal antheridia of the same slide, three showed the nucleus clearly and three failed to show it. Of three others chosen for the sharp definition of the cap cells, the nucleus could be identified in all. A fourth successive antheridium showed the green granular mass with a nucleus but no cell wall. This fourth antheridium seemed to have a lunate cap cell in place, thus providing another example of a divided cap cell seen in *A. filix-foemina*.

It is therefore apparent that the distinctness, as well as the condition, of the detached cap cells varies. The observed range of possibilities is illustrated in the photomicrographs of *Athyrium filix-foemina*. Figs. 23 and 26 show typical detached cap cells in good condition. The nucleus is especially distinct in fig. 23. In fig. 22 the detached cap cell is also typical, but the cell content is somewhat degenerated. As a third possibility, fig. 21 shows the extruded granular matter which represents cap cell content. The additional variation, that of the tilted or partially detached cap cell, is illustrated for *Onoclea sensibilis* in fig. 19. The pore or hole in the outer membrane through which the cap cell passes is evident in fig. 22.

A discussion of the microchemical investigations is to follow, but, summarizing the morphological work, the following facts have been observed:

I. The cap cell is regularly undivided in the polypod species studied, except *Woodsia obtusa*, where division is frequent, and *Athyrium filix-foemina*, where it is occasional.

II. Extrusion of the intact cap cell is a frequent method of antheridial dehiscence in many polypod species: *Onoclea sensibilis, Aspidium marginale, Aspidium simulatum, Polystichum acrostichoides, Athyrium filix-foemina, Woodsia obtusa, Dennstaedtia punctilobula, Microlepia platyphylla.*

Extrusion of the intact cap cell is an almost unvarying method of dehiscence in certain species, as *Athyrium filix-foemina* and *Microlepia platyphylla*.

III. When the cap cell is divided, extrusion of one of the daughter cells is usual, as in *Woodsia obtusa* and *Athyrium filix-foemina*.

IV. Extrusion of the intact cap cell occurs at least occasionally in other species: *Davallia pentaphylla*, *Adiantum pedatum*, *Woodsia ilvensis*, *Cyrtomium falcatum*, *Woodwardia orientalis*.

V. Tilting of the cap cell, sometimes found in place of complete extrusion, is equivalent to it and may become identical, as in *Onoclea sensibilis*.

VI. In a given species, the frequency of total extrusion of the intact cap cell may vary, apparently with physiological or cultural conditions, as observed in *Onoclea sensibilis* and others.

VII. In the absence of the intact detached cap cell, an extruded green granular mass is frequently seen, as in: *Polypodium aureum*, *Woodsia ilvensis*, *Onoclea sensibilis*, *Cyrtomium falcatum*, *Woodsia obtusa*, *Woodwardia angustifolia*, *Athyrium filix-foemina*, *Polystichum acrostichoides*.

VIII. This granular mass bears a striking resemblance to the content of the extruded cap cell, in that: (a) it contains green granular material analogous to the decomposing chloroplasts seen in some of the detached cells (*Woodsia ilvensis*, *Onoclea sensibilis*, *Athyrium filix-foemina*); (b) it sometimes contains a well defined nucleus (*Woodsia obtusa*, *Onoclea sensibilis*, *Athyrium filix-foemina*); (c) it is extruded before the spermatogenous mass (*Cyrtomium falcatum*, *Woodsia obtusa*, *Woodwardia angustifolia*).

IX. The nucleus may be invisible even in the intact extruded cell (*Athyrium filix-foemina*).

X. There is, regardless of cap cell behavior, a hole in the outer membrane of the antheridium, as seen in most species studied.

XI. Swelling of the spermatogenous mass is an important factor, and probably the primary agency, in causing rupture of the outer membrane, as seen especially in *Aspidium simulatum*.

XII. Intrusion of the ring and basal cell effects extrusion of the spermatocytes, as seen in all species.

These observed facts support the following conclusions:

1. Detachment of the intact cap cell (complete extrusion or mere tilting) is a general method of antheridial dehiscence in the Polypodiaceae.

2. Extrusion of green granular material represents extrusion of cap cell content.

3. These two types of dehiscence are therefore essentially one, namely, an extrusion of the opercular cell with or without the intact inner membrane.

4. A star-shaped rupture of the apical cell, in the sense of the earlier writers, does not occur.

5. The wall cells are active in antheridial dehiscence, although swelling of the spermatogenous mass seems to be primary in causing the initial opening: (a) the cap cell, or its daughter cell, forms at maturity a detachable operculum; (b) the basal cell aids in the pressure which causes rupture of the outer membrane; (c) the ring and basal cells, by their inward protrusion, eject the spermatogenous mass.

A reconstructed general view of antheridial dehiscence in the Polypodiaceae may then be given, as follows:

When the mature antheridium has access to water, the spermatogenous mass swells until its pressure, probably aided by that of the basal cell, causes rupture of the outer membrane (original wall) of the antheridium. The opercular cell, with or without its inner wall intact, is then extruded or sometimes merely tilted, and the spermatocytes follow, being pushed out chiefly by force of the intrusion of the ring and basal cells. The opercular cell is regularly the undivided cap cell; but frequently in *Woodsia obtusa*, and sometimes in *Athyrium filix-foemina*, it is a daughter cell of the original cap cell.

Microchemical investigations

The series of tests outlined by ECKERSON (10) were used for the microchemical studies. As occasion arose, this outline was supplemented by general works, such as those of TUNMANN (34), MOLISCH (22), HAAS AND HILL (14), THATCHER (31), ONSLOW (24), and HAWK (15), as well as by detailed research papers.

The tests were performed repeatedly, and were checked as far as

possible, either with the pure chemical or with plant parts known to contain the substance in question. Although this work is not exhaustive, interesting data are available.

The walls of the gametophyte, including those of the antheridia, are partly pectic in nature, as shown by the ruthenium red color test. For example, when gametophytes of *Athyrium filix-foemina* are mounted in water and then treated with ruthenium red, the following reaction is obtained:

A. VEGETATIVE PARTS:

1. Rhizoids stain vividly.
2. Prothallial cell walls stain.
   a. In the old degenerating portion near the spore.
   b. In the healthy tissue where a tear occurred.

B. ANTHERIDIAL PARTS:

1. Freshly opened antheridia.
   a. Ring and basal cells become pink: (1) diffusely pink throughout; (2) deeper pink, frequently, along upper wall of funnel cell and inner and upper walls of ring cell.
   b. Detached cap cells stain: (1) sometimes more vividly than the other cells; (2) sometimes less vividly.
   c. Sperm mother cell membranes stain; the sperm within remains colorless.
   d. Vesicles of freed sperms may stain slightly.
   e. Nuclei sometimes stain in: (1) ring or basal cell; (2) detached cap cell; (3) granular mass of extruded cap cell contents.
2. Old open antheridia.
   a. The central cavity stains vividly.
3. Unopened antheridia.
   a. Usually stain slightly or not at all.
   b. If accidentally torn from the thallus, the spermatogenous mass stains vividly (detachment apparently favoring penetration of reagent).

Similar results were obtained with the other species studied, *Aspidium simulatum*, *Polypodium iroides*, *Davallia pentaphylla*, *Onoclea sensibilis*, and *Cyrtomium falcatum*, but the observations were not in every case as full as those just outlined. The test is less defi-

nite if gametophytes are mounted directly in a weak aqueous solution of ruthenium red, although the antheridia are capable of opening in this medium. In check tests with methylene blue only *Athyrium filix-foemina* and *Aspidium simulatum* were used.

Solubility tests, following ECKERSON (10), (cf. TIFFANY 32, HOWE 18, and ROBERTS 26), indicate that the walls probably contain pectose, as they fail to restrain after treatment with dilute hydrochloric acid. The pectic materials of the rhizoids, however, are often resistant to both acid and alkali. The sperm mother cell membranes seem to be pectin, as they dissolve in water. The nature of the pectic material of the cap cell remained undetermined, as the manipulations of the solubility tests repeatedly caused loss of this cell.

The swelling of a slime in which the sperm mother cells are imbedded has been suggested as a factor important in the opening (SCHLUMBERGER 28, HOFMEISTER 17, BAUKE 2). This study indicates that swelling of the spermatogenous mass results from the pectin of the sperm mother cell membranes. It may be that a pectose or pectinogen is converted by hydrolysis into pectin during the ripening process (cf. HAAS and HILL 14, ONSLOW 24, THATCHER 31 on pectic substances). Other factors, such as the possible presence of a trace of pectin from the dissolution of the middle lamella of the cap cell, may act in the mechanism. As to the swelling of the peripheral cells, it is not wholly certain whether the pectic materials found in them are identical with the hyaline slime found by SCHLUMBERGER (28) in his use of ruthenium red. This slime is also emphasized by GOEBEL (13) in explaining the activity of the wall cells.

The walls of the gametophyte, including those of the antheridia, are also partly cellulose in nature. In general, the usual cellulose tests were positive, although there was some variation in results. This variation probably was caused, in part at least, by the presence of other substances with the cellulose. With the usual iodine sulphuric acid color test, best results were obtained with the following modification of the procedure suggested by ECKERSON (10):

a. Limitation of the reaction period in the iodine potassium iodide solution to approximately 10 minutes.

b. Addition of a drop of water with or immediately following the

sulphuric acid (specimens mounted first in water were touched to filter paper before being transferred to a drop of the iodine solution).

The results were as follows:

A. VEGETATIVE PARTS:

1. Prothallial cell walls become blue.
2. Rhizoids become blue.
3. Walls of prothallial hairs become blue.

B. ANTHERIDIAL PARTS:

1. Antheridium in general becomes blue: (a) it may be bluer at base than at apex; (b) basal cell may be decidedly more blue than ring cell; (c) detached cap cell may shrivel or swell on addition of sulphuric acid (or shrivel and expand again); (d) detached cap cell fails to become blue, in one case it became slightly blue; (e) young antheridia fail to become blue, although adjacent prothallial walls are blue.

The following species were used in these tests: *Aspidium simulatum*, *Cyrtomium falcatum*, *Athyrium filix-foemina*, *Onoclea sensibilis*, *Polystichum acrostichoides*, and *Polystichum aculeatum*. Again the more detailed work was done with *Athyrium*. However, no consistent variation of reaction was found for any given species. The use of iodine-zinc chloride (HAWK **15**, after NOWOPOKROWSKY) was confirmatory of these results, in that antheridial and prothallial walls became blue in this reagent. Additional iodine potassium iodide was used, until the reagent would color tissue from *Capsella*.

The presence of cellulose was further verified by means of crystallization. With a gametophyte of *Athyrium filix-foemina*, cellulose crystals were obtained which compared favorably with those shown by MOLISCH (**22**). The crystals in the prothallial cells were more distinct than those about the antheridia.

Solubility tests were also made, and again *A. filix-foemina* was used. After several days in ammoniacal copper oxide, gametophytes stained a reddish blue when placed in the iodine reagent. This bluing seemed to involve cell contents rather than cell walls. Addition of sulphuric acid removed the blue. The residue from these tests gave a strong pectic reaction.

With polarized light, the presence of cellulose in gametophytes of *A. filix-foemina* was indicated as follows:

A. VEGETATIVE PARTS:

1. Prothallial cell walls strongly anisotropic.
2. Walls of rhizoids also anisotropic.

B. ANTHERIDIAL PARTS:

1. Outer membrane of antheridium: (a) this wall is strongly anisotropic, even in young antheridia; (b) isotropic spermatocytes were seen passing out through the opening in this luminous membrane; (c) in only one case did this membrane appear to be lacking in cellulose (isotropic), and then merely in the extreme apical portion.
2. Cap cell: (a) cap cell is frequently wholly isotropic; (b) in two cases, an extruded cap cell appeared to have a trace of cellulose at each end.
3. Ring cell: (a) this cell varied in luminosity in different antheridia, but appeared to contain relatively little cellulose.
4. Basal cell: (a) basal cell also varied in luminosity, but frequently appeared to have more cellulose than ring cell; (b) in some cases it appeared to lack cellulose only in the central portion of its upper wall; (c) in one case the upper wall was luminous throughout; (d) in two other antheridia, one very young and one approximately mature, the basal cell, exclusive of the outer membrane, was lacking in cellulose.

The distribution of cellulose would seem to be significant, as it is conspicuously present in the resistant outer membrane of the antheridium, almost wholly lacking in the cap cell itself, and sometimes conspicuous in the basal cell. The variability of its presence is also suggestive. Probably the lack of cellulose in the cap cell is largely responsible for the evanescent nature of its membrane.

To what extent the non-cellulose walls are pectic in composition, and to what extent the cellulose itself exists in combination with other substances, is not certain. However, the fact that gametophytes of *Athyrium filix-foemina*, soaked in Javelle water (as suggested by Dr. PAUL B. SEARS) from one to several days, gave exceptionally good bluing in the hydrocellulose reaction, indicates the presence of a combined cellulose. It appears that the Javelle water dissolves out certain wall constituents that otherwise hinder the hydrocellulose reaction. Identification of these interfering sub-

stances has not been made. Pectic materials are known to be present; protein might well be expected in these young walls; and fatty materials offer a third possibility.

TUPPER-CAREY and PRIESTLEY (35) have studied in detail the cellulose reactions of young walls. They suggest protein complexes as responsible in certain cases for resistance to sulphuric acid, while fatty substances may inhibit the reaction with chloriodide of zinc. They used Javelle water to dissolve out cell contents, but do not suggest that it dissolves the complex protein of the walls, unless followed or preceded by ammonia, in which case it would also remove interfering fatty substances. The conclusions of TUPPER-CAREY and PRIESTLEY were further supported by an experiment involving digestion with enzymes.

Protein tests have been made with *Athyrium filix-foemina*, but without special reference to the walls. Positive reactions were obtained with Millon's reaction and the xantho-proteic reaction. The biuret reaction was very faint. The color in each case was in the spermatogenous mass. It is recognized that certain other substances could give these reactions.

Tests for fatty substances have involved primarily the tests for cutin. Although gametophytes from a number of species were tested, the results were hardly convincing and were in general negative. The walls of rhizoids and antheridia of *Athyrium filix-foemina* were resistant to a 3-day period in concentrated sulphuric acid at room temperatures. Sudan III occasionally gave a slight reddishness of the membranes, as checked with the use of compensating ocular and apochromatic objective. Saponification tests have been negative; but a separation of the wall into two layers was noted about the antheridia and marginal prothallial cells. The use of osmic acid indicated the presence of diffuse fatty material in the prothallial cells, the peripheral antheridial cells, and particularly at the apex of a young antheridium. The reagent was used as suggested by GARDINER and ITO (11) for a tannin test.

Pentosan tests were also made. The usual tests with orcin or phloroglucin were negative, or occasionally indicative of the presence of a trace of pentosan material. With Matthew's orcin, on the contrary, a dull brick red (that is, a pale color with red predominat-

ing but having also a blue quality) was obtained regularly in the spermatogenous mass of antheridia of *Onoclea sensibilis*, *Cyrtomium falcatum*, and *Aspidium simulatum*, when heated several minutes on the boiling water bath.

When gametophytes of *Athyrium filix-foemina* were hydrolyzed for an hour or more (over the boiling water bath) with 20 per cent hydrochloric acid, a reddish color developed which became most conspicuous about the sperm mother cells. The use of either orcin or phloroglucin (as in the usual pentosan tests) increased the intensity of this color, indicating that the hydrolysis liberates pentoses (possibly from the pectic materials present), and that the gametophytes and particularly the antheridia contain some substance capable of giving the color reaction with the pentoses (probably a phenol). Tests for galactan were also made. With *Cyrtomium falcatum* and *Athyrium filix-foemina*, insoluble colorless crystals were obtained which compared favorably with those similarly prepared from agar-agar, and with those of pure mucic acid. After hydrolysis with hydrochloric acid, many crystals of cuprous oxide appeared with Flückiger's reagent. There seemed to be more of this precipitate in hydrolyzed than in unhydrolyzed material, possibly indicating a breaking down of hemicelluloses into sugars. Accurate quantitative work was not done.

A general mucilage test was made, using methylene blue as suggested by YOUNGKEN (38). The thalli were mounted in the reagent for 3 minutes, lifted out and touched to filter paper, mounted in glycerin and observed. The results were as follows:

A. FIRST OBSERVATION:
   1. Spermatogenous masses very blue.
   2. Peripheral cells slightly blue.
   3. Prothallial cells not blue.
   4. Rhizoids blue.

B. LATER OBSERVATION (several hours later, after the excess blue had faded out):
   1. Spermatogenous mass a deep purple blue, darker at base of funnel.
   2. Peripheral cells a decided light blue.
   3. Rhizoids a similar light blue.

The additional tests made included those for tannins, starch, and sugars.

For starch, the iodine reagent was used. Starch granules were found in the sperm mother cells, apparently in the vesicle of the sperm cell. Their presence has been noted in the sperms of various ferns by BULLER (6), MOTTIER (21), ALLEN (1), and CAMPBELL (7). Starch was also frequently found associated with the chloroplasts of the peripheral cells of the antheridium, but sometimes was lacking. These chloroplasts are regularly smaller than those of adjacent prothallial cells. The gametophytes used included the following species: *Cyrtomium falcatum*, *Onoclea sensibilis*, *Aspidium simulatum*, and *Woodwardia orientalis*. It is interesting to note that the basal cell sometimes became browner than the other cells, in the iodin reagent.

The observation of many granules in the cytoplasm of the peripheral cells during the starch tests suggested the possibility of the presence of tannin. The osmic acid test after GARDINER and ITO (11) was first used. The results were indefinite, but in general negative. Later the tannin tests outlined by ECKERSON (10) were used, and supplemented by other tests suggested by HAAS and HILL (14). Most of this work was done with prothallia of *Onoclea sensibilis*. In general, the presence of a trace of tannin was indicated.

Sugars are present in the antheridia as indicated by Flückiger's reaction. The cuprous oxide crystals of the fern material appeared in clusters or balls rather than being scattered, as in tests with the pure sugars. Enough copper tartrate was used to make the drop of solution decidedly blue. Good localization was obtained about the antheridia of *Onoclea sensibilis*, after one minute's heating on the water bath. The crystals were particularly abundant about the cap cell (fig. 20). At least 73 antheridia on one slide gave a localized test. Longer heating gave scattered crystals, especially abundant among the rhizoids. With *Cyrtomium falcatum* the crystals were most conspicuous on the ring cell, but also abundant about the cap cell.

Osazone tests were also made, but definite identification of the sugars present is not possible at this time. Drawings of osazones appear in figs. 8–10, on antheridia of *Onoclea sensibilis*. Osazones were also obtained on antheridia of *Cyrtomium falcatum*.

Whether these sugars function in an osmotic mechanism that causes the swelling of the peripheral cells of the antheridium cannot be determined without further study.

General summary

1. This investigation of antheridial dehiscence in the Polypodiaceae was based on living material, both morphological and microchemical studies being made.

2. Extrusion of the intact cap cell has been found to be a characteristic method of antheridial dehiscence, as described by SCHLUMBERGER.

3. One significant modification of the extrusion of the cap cell has frequently been observed, the extrusion of cap cell contents as a granular mass.

4. In all cases there is a hole or pore in the outer membrane of the antheridium.

5. A star-shaped rupture of the apical cell, in the sense of the earlier writers, does not occur.

6. The wall cells are active in the opening; but the swelling of the spermatogenous mass seems to be primary in causing the initial tear in the outer membrane.

7. The pectin of the sperm mother cell membranes seems to cause swelling of the spermatogenous mass.

8. The wall cells are also partly pectic in nature, a fact which may account, at least partially, for their ability to swell.

9. The cap cell is markedly lacking in cellulose, a fact which may account for the observed evanescent nature of its inner membrane.

10. The presence of sugars in the peripheral cells is indicated.

11. *Athyrium filix-foemina* should be added to the list of polypod species in which the cap cell of the antheridium sometimes becomes divided.

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DEVELOPMENT AND VASCULAR ORGANIZATION OF THE FOLIAR ORGANS OF CARYA CORDIFORMIS

LaDema M. Langdon

(WITH PLATES I, II AND FOUR FIGURES)

Introduction

This paper, continuing an investigation in seedling anatomy first reported in 1927 (**12**), presents the results of a somewhat detailed study of the development of foliar organs in *Carya cordiformis*, with particular emphasis on the origin and differentiation of the vascular tissues of the leaf and scale primordia of seedling buds.

A great number of papers have been published relating to the subject of foliar morphology since the studies of de Candolle (**1**), Nageli, and Trecul; but in these earlier accounts, references to the origin and longitudinal differentiation of the vascular tissues of the leaf, or exact relation of the foliar strands to the organization of the primary vascular axis, have been indefinite and often contradictory. Concerning the position of meristem in the leaf, Nageli (**13**) early established from his examination of certain of the phanerogams (*Utricularia*, *Astragalus*, and *Myriophyllum*) that the leaf possesses originally an apical vegetative point; but this may be the first to pass over into permanent tissue, while at the base of the leaf cell formation takes place freely, inasmuch as the tissue there retains its embryonal character.

Trecul (**15**) found that development of lateral members of a leaf may proceed sometimes acropetally, sometimes basipetally, or from the middle both upward and downward; further, that this process of leaf formation may show variance in different although closely allied plants. His error in considering that the leaf sheath was the first to arise was later corrected by Eichler (**5**), who found that the base of the leaf does not at once take on the character of the leaf sheath, but the sheath is differentiated later only by intercalary growth out of the basal portion of the leaf.

With regard to the laying down of the leaf surface, PRANTL (14) distinguished three types of leaves: (1) Those of the basiplastic type, where the stretching takes place at the apex of the primarily uniform embryonal primordium, and proceeds downward until nearly the whole of the active meristem disappears. This is found in the Musci, *Lycopodium*, Coniferae, most monocotyledons, and a number of dicotyledons. Where, as in dicotyledons, feathered veins occur, a strong midrib is first of all differentiated, and this is accompanied both right and left by meristic tissue, which passes over into stretching tissue successively in a basipetal direction, and at the same time in a transverse direction. (2) In the pleuroplastic type, where the meristem is marginal, the leaf apex does not pass into the permanent condition as rapidly as in the basiplastic type. The transition into stretching tissue takes place in the whole tissue arising out of the meristem at nearly the same moment. When branchings occur they proceed in acropetal succession, as in *Quercus*, *Corylus*, and *Tilia*. (3) In the eucladous type the branchings do not proceed, as in the two former types, only when a portion of the meristem has commenced to stretch, but appear when the leaf is still one uniform mass of embryonal tissue. This is seen in *Ginkgo*, *Juglans*, and the Papilionaceae.

Of the later publication dealing with the ontogeny of foliar organs of the dicotyledons, those of FOSTER (6) are the most recent and most detailed. In his studies of the periodicity and comparative history of development of the foliage leaves and cataphyllary structures of the horse-chestnut, he concludes that the bud scales and the lower transitional forms in *Aesculus* are two-membered foliar organs in which the variously developed "lamina" is homologous with the blade of the foliage leaf; while the characteristic and polymorphic sheath is essentially a winged structure, and represents a completely divergent product of the "hypopodium" (leaf base). GOEBEL's theory of "arrested formations" he finds inapplicable to the situation in the horse-chestnut, and concludes that the cataphyllary structures develop from primordia in which there is an almost complete reversal of the growth rates existing between the lamina and the "hypopodium" in the foliage leaf initial.

The problem of distribution and order of appearance of the veins

(primary and secondary) of the leaves of monocotyledons and dicotyledons has been dealt with in some detail by most of the writers mentioned here and others, but in practically all accounts a vague but commonly accepted theory is that leaf traces, vascular strands connecting the vascular supply of the blade with that of the stem axis, are "put forth" at different points from the vascular cylinder, and differentiate toward the leaf. In their progress through the sheathing leaf base they meet and anastomose, or branch freely, eventually becoming continuous with the primary vascular supply of the petiole and lamina.

TRECUL (**16**), in his study of venation in the leaves of *Aesculus*, describes the primary bundle of the scales as ascending from the stem and progressing toward the median leaflet. Other primary bundles arise a short distance to either side, successively beneath the first and second lateral leaflets, and elongation of these bundles in the leaflets is from base to apex. Secondary bundles arise later, interposed between the primary bundles (later connected with them), and in their passage toward the tip of the scales they fork, supplying branches to adjacent ribs of neighboring leaflets.

The venation typical of monocotyledons arises according to GOEBEL (**7, 8**) "when a primordium of a leaf attached by a broad base to the stem, grows nearly uniformly in length and breadth (but at different times)." The conducting bundles which "enter" the leaf, and out of which the median is formed, traverse its whole length nearly uniformally from base to apex. Among the dicotyledons two cases cited are: (1) that of *Acer platanoides* (a palmate leaf with a divergent type of primary veins), where the middle nerve enters the leaf first, then in order the veins of the two upper and two lower leaf lobes; (2) that of *Fraxinus excelsior* (a pinnate leaf with acropetal succession of pinnules), in the broad base of the leaf primordium of which a large number of conducting bundles radiate from one another in correspondence with the growth of the pinnules. No precise information is given in either case as to the point of origin or direction of differentiation of the primary laminar bundles.

According to EAMES and MACDANIELS (**4**), the term leaf trace may be applied to any bundle which extends to a leaf, or to the complex of bundles supplying a given leaf. In *Quercus* and *Carya*, I have

found that origin and longitudinal differentiation of the procambial or desmogen elements composing the leaf trace commence in the leaf base, and progress from that point basipetally until they meet and merge in the primary vascular axis with like elements of other traces. This seems to be in agreement with HABERLANDT's (**9**) observations regarding the "dicotyledonous type" of vascular structure.

Investigation

MATERIALS AND METHODS

For the purposes of the major part of this study, seedlings of *Carya cordiformis* 3–8 weeks old, with plumules ranging from 2.5 mm. to 6 cm. in length, were selected; and, as in the case of *Quercus* (**12**), serial paraffin sections were secured through the plumules from tip of main axis to the cotyledonary plate. Dissections of seedling buds were to some extent used to supplement the serial preparations, successive scale and foliage leaves being removed with the aid of needles, cleared in alcohols and xylene, and mounted in damar. When examined with a binocular microscope (16 mm. obj. and 5 oc. combination) under strong artificial light, considerable internal as well as external detail is distinguishable in these cleared preparations.

Fixation of the sectioned material was with formalin-acetic-alcohol (**2, 11**) or with Flemming's fluid (weaker solution). Sections were cut 8–10 μ, and staining in practically all cases was with safranin-light green or with Flemming's triple stain, the latter proving most satisfactory in the differentiating of meristematic tissues.

The foliar organs, formed by the primary axis of seedlings of the stages just described, consist of 6–8 scale leaves, and 5–6 foliage leaves and primordia. The transition from scale to foliage leaf may be regarded as somewhat gradual, for the first-formed foliage leaf is reduced to one leaflet (with at times the rudiments of two others), while the scale leaves immediately preceding the first foliage leaf display a marked, although reduced, laminate structure.

The scale and foliage leaves from their early stages of development are more or less completely enveloped in a dense tangle of hairs: unbranched unicellular, multicellular protective, and glandular. The latter, illustrated in different figures of this paper, are of several types. Some are unicellular or small multicellular, short-

stalked, capitate glands (figs. 7, 8, 10, 12), their secreting cells thin-walled, rich in protoplasm, and but slightly vacuolate, very likely early stages in the development of larger glands; others are mucilage or resin-secreting glands of an elaborate type (figs. 8, 9, 11, 14, 21), consisting of a base and a one-two-celled stalk surmounted by a multicellular cup- or disk-shaped gland. In such mucilage or resin-secreting glands, according to VON HANSTEIN (10), the secretion is generally a constituent of the cell membrane, appearing in a constantly increasing quantity between the cuticle and the cellulose layers of the wall, until the cuticle is distended in a vesicular manner and finally ruptured. Whether the raw materials from which the secretions are made are derived directly from the cell contents, however, or entirely from metamorphosed layers of the cell membrane, is a question as yet undetermined.

Both the glandular and the protective hairs may offer some impediment to sectioning, particularly the protective hairs on the older scale and foliage leaves, owing to their thickened walls and the accumulation within their cells of resins and tannins. The same difficulty is encountered in the preparation of oak buds; here, however, the problem is further complicated by the unyielding and brittle protective stipules.

MERISTEM AND PRIMARY TISSUES OF AXIS

Cases of terminal growth by means of several apical cells, such as characterize the leaf stems of the majority of angiosperms, have been considered in some detail by several investigators, including HANSTEIN (10), DOULIOT (3), and HABERLANDT (9). HANSTEIN distinguished in the stem tip of certain of the dicotyledons three distinct strata or "histogens," giving rise to the plerome, periblem, and dermatogen. These histogens are reported to appear at the first divisions of the embryo, maintaining their independence throughout the life of the plant, and are increased each by its own group of initials. DOULIOT, whose work on terminal growth (3) has already been reviewed (12), appears to have placed more emphasis on a "vertical" series of generative cells in dicotyledons, 2–3 initials superimposed from which epidermis, cortex, and central cylinder are derived.

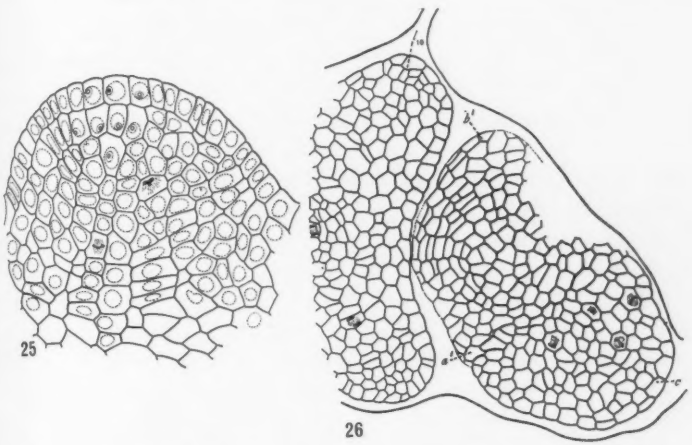
HABERLANDT has summarized the three possible ways in which

several initials may be associated as follows: (1) two to several apical cells all located in the same horizontal plane, juxtaposed or horizontally seriated; (2) apical cells (2 or 3 in number) situated in successive horizontal planes, superimposed or vertically seriated; (3) cases where the apical cells are arranged in successive strata (that is, both juxtaposed and superimposed). This third type is by far the most difficult of observation, but probably widely distributed among angiosperms.

SEEDLINGS.—With the appearance of the first foliar organs, the terminal apices of *Carya* seedlings are so complicated by rapidly forming primordia that it becomes difficult to distinguish the vegetative point and initials of the stem from the generative cells of the youngest leaf primordia. In certain of the younger axillary shoots of the seedling, however, as well as in the primary axis of winter buds of this genus, it has been possible to distinguish a stem tip. In fig. 25, a median longitudinal section through a young axillary shoot of a seedling of *Carya cordiformis*, there appear two successive horizontal groups of initials and a single basal initial, the 3 units associated at the apex of the stem's axis in the form of an inverted cone or wedge. The initial cells of the upper series, 3 or 4 in number, from which the dermatogen is derived, all meet at the center or adjoin the median plane of the axis. Immediately beneath these can be seen a second series of 4 initials from which by periclinal divisions a cortical section of the stem is derived; and at the apex of the wedge a single large 6-sided initial, with 5 cutting faces, one basal and 4 lateral, from which the central portion of the stem's promeristem takes its origin. A stratification of the meristem due to this vertical seriation of the initials is evident for only a short distance behind the apex. It soon becomes difficult to determine just how much of the promeristem may be traced to the second series and how much to the single basal initial. Fig. 26, surface view of a portion of the stem tip and 3 primordia of the primary axis of a winter bud, demonstrates the arrangement of the upper series of initials of the stem axis, as also the relation of segments cut from these initials.

Figs. 3, 4, 7, 10, and 11 are representative of conditions found at different levels in the primary axis of *Carya* seedlings. Fig. 3, a transverse section just above the tip of the axis, shows in outline the

petioles of four leaves and the bases of the primordia of a fifth and sixth foliar appendage. Fig. 7 shows in detail a section of the primary axis at the level of the stem apex and slightly above the point where the youngest primordium (L_6) merges with the stem tissues. In this region there appear, distinctly outlined, six small masses of procambial tissue, five of which are associated with the base of the fifth or second youngest primordium, while strand *ms* marks the position of the central or first procambial strand of the sixth or youngest primordium. The three median primary strands of the fifth leaf are



FIGS. 25, 26.—*Carya cordiformis:* fig. 25, median longitudinal section through young axillary shoot of seedling, showing promeristematic tissue and vegetative point of stem; ×533; fig. 26, surface of apex of primary axis of winter bud, showing portion of stem tip and three primordia (a', b', c'), also section base of tenth leaf; ×229.

seen drawing toward the center; also the left and right lateral primary strands of the same primordium.

At the second node from the apex (fig. 10), a point 48 μ below that illustrated in fig. 7, there is a well organized primary vascular cylinder, interrupted only by the promeristematic tissue of a secondary shoot borne in the axil of the fourth leaf. All elements of this primary cylinder, as yet in the procambial condition, have their origin at the bases of primordia enveloping the axis; and in the course of

their basipetal differentiation they enter the primary vascular cylinder, becoming its "common" bundles.

The foliar origin of the procambial elements of the primary vascular axis is also apparent in fig. 11, detailing the basal portion of the fourth leaf at its point of union with the stem. The primary laminar strands (lateral and median) mark the position of the 4 or 5 outward projecting points or ridges of the primary cylinder, while the desmogen strands (described as taking their origin concurrent with that of the primary traces, but in the extreme lower section of the primordial leaf base and differentiating chiefly basipetally) occupy the slightly depressed regions of the cylinder. The latter (*a*, figs. 10, 11), although clearly defined at the second and third nodes from the apex, are still undifferentiated procambium. At the fourth and fifth nodes these connecting strips of primary vascular tissue can be distinguished as discrete bundles occupying the areas between the median and lateral primary traces, but maturing later than the primary laminar strands (figs. 5, 24).

Foliage leaf

The foliar organs of *Carya cordiformis*, both foliage and scale leaves, are arranged alternately in 5 vertical ranks on the stem axis, with the sixth over the first, the seventh over the second, the eighth over the third, etc., the usual 2/5 leaf arrangement so common in alternate-leaved dicotyledonous plants.

Each adult foliage leaf of the seedling consists of a leaf base (conspicuously sheathing), a petiole, and a lamina of 1–5 broadly lanceolate, slightly stalked leaflets, pinnately arranged. The number of leaflets forming the lamina of the adult foliage leaf in winter buds ranges from 7 to 9 or even 11. It is evident, therefore, that considerable variability in leaflet number occurs both in seedling and winter buds of *C. cordiformis*.

In seedlings 6–8 weeks old, the lamina of the first-formed foliage leaf frequently consists of but a single leaflet. The second, third, and fourth in order of appearance are usually tripinnate (figs. 1–3), while the fifth bears the primordial lobes of five leaflets, and the sixth and seventh are each unilobate. In younger seedlings (3–4 weeks old) the lamina of the first foliage leaf is also unipinnate, the

second may be bi- or tripinnate, the third tripinnate, the fourth displays 3–5 leaflet primordia, while the fifth and sixth are each unilobate. In the foliage leaves of winter buds there is an increase in number of leaflets (7–9) with successive leaves, that is, to the sixth leaf; but in later-formed leaf primordia, a decrease from seven to five or even three leaflet primordia. The last two sets of primordia borne at the stem tip are apparently primordia of scale leaves.

FOSTER (**6**) has pointed out that the number of leaflets in the adult foliage leaf of the horse-chestnut decreases with each successive pair of leaves, while in the cataphyllary series there is noted a tendency for the number of leaflet primordia to increase progressively from five in the lower scales to seven in the upper cataphylls. The causal factors responsible for this fluctuation in leaflet number, as well as the asymmetrical formation of leaflet primordia, he believes are completely obscure.

DEVELOPMENT OF PRIMORDIUM.—No exact determination of the number and arrangement of the generation cells of the leaf of *Carya* has as yet been made, although the preparation of embryonic stages essential for such a determination is in progress.

The foliage leaf primordium makes its appearance as a small, knoblike emergence, which by rapid meristematic growth soon extends as a ridgelike papilla on either side of the slender vegetative point to about one-half the circumference of the axis. The bases of the two youngest primordia not only meet but in some cases actually merge above the growing point. After the formation of the first scale leaves, so closely do these primordia succeed one another that it becomes practically impossible to distinguish the vegetative point or promeristematic region of the stem from the youngest primordium of a leaf. In vegetative points with such close-set primordia of leaves, GOEBEL (**8**) observed that not infrequently there is no free surface of the growing point left, and in such cases the lower portion of the leaf primordium remains frequently united with the surface of the shoot. There follows a period of general and rapid meristematic growth in the primordial leaf, in the course of which the lobes of the first primary segments of the lamina appear, the median one first and well in advance of the first laterals. It is the writer's observation that subsequently formed lateral leaflet primordia in the foliage or-

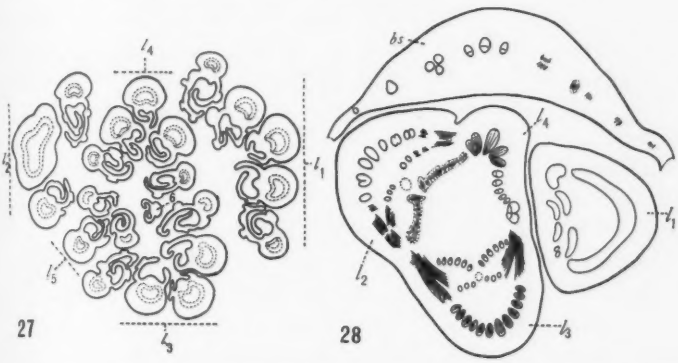
gans arise when the central portion of the embryo leaf has commenced to stretch, and appear as successively developed lateral lobes on the marginal meristems of the "upper leaf." With the formation of the first two lateral leaflet primordia, primary segmentation or development of leaf members of the first order may cease, as is the case in the scale and first three or four foliage leaves of the seedling.

If other leaflet primordia are formed, they appear in acropetal succession, the primordium of the third leaflet above the first lateral, the fourth above the second lateral, etc. The leaf primordium at this point (fig. 18 P_6) consists of a diminutive base, and a 3–5-lobed lamina with no evident elongation of the zone between the leaf base and the blade. Stretching commences at the apex of each embryonic leaflet, and proceeds downward with early differentiation into midrib and marginal meristems (fig. 19). The median or first-formed leaflet may have progressed to this stage of differentiation while the laterals are still blunt, uniformly embryonic projections. Marginal teeth take their origin at a later period as lateral projections from the marginal meristems of each leaflet.

Differentiation of the desmogen or procambial elements of the primary vascular bundles takes place early, and is first evident in the primordial leaf base. As stated previously (12), the elements of these strands may be distinguished from the surrounding tissues by the size and shape of the cells and the character of mitotic activity. In an embryonic leaf consisting of three leaflet primordia, differentiation of procambium occurs at three points in that region of the primordium destined to become the upper section of the leaf base. The first strand appears while the primordium is still in the unilobate condition, as a group of desmogen elements occupying a central position beneath the median leaflet lobe. Other primary strands arise later, with the evolution of lateral pinnae, one beneath each of the primary lateral leaflet primordia.

With continued meristematic activity in the basal section of each leaflet primordium, "secondary" desmogen strands (varying in number) arise to either side of the differentiating primary strands. The progression in development of these several groups of strands (both primary and secondary) is from their point of origin both acropetal

and basipetal. Acropetally they enter the five primordial lobes of the leaf, and their further development in this direction keeps pace with the growth of the leaflets, the median "primary" strand of each group being the center bundle of the primary midrib of each leaflet. Basipetally the differentiation of the desmogen strands progresses by repeated longitudinal division of the intervening elements of the leaf base and cortex of axis. In their basal differentiation there occur in the upper section of the leaf base an approximation and anastomosis of the primary and secondary strands of each leaflet, so that



FIGS. 27, 28.—*Carya ovata:* fig. 27, transverse section of upper portion of winter bud; pinnae of six of oldest foliage leaves illustrated; ×17.8; fig. 28, transverse section through basal portion of same bud, showing vascular organization of basal sections of second and third leaves, and connection of vascular strands of fourth leaf with primary axis; ×29.8.

the several bundles ordinarily found at the base of the petiole are reduced to a median group of 3–5 bundles, and two lateral groups each consisting of 1–3 strands; and thus, as three separate groups, they approach and connect with the primary vascular axis (figs. 4, 5, 10, 11, 28).

While differentiation of the procambial elements of the "primary" bundles of the leaflet primordia is in progress, there may be distinguished in the broadening leaf base the desmogen of yet another set of vascular strands. These strands (5–9 in number) take their origin at a lower level in the leaf base than strands supplying the

lamina of the leaf, and differentiate acropetally only to a point of union with the median and lateral laminar bundles. Basipetally they maintain a direct and independent course (*a*, figs. 10, 11, 24), entering the primary vascular axis to either side of the median laminar strands. Such bundles occupy that portion of the leaf base extending between the median and lateral primary laminar groups, and upon entering the primary cylinder occupy the slightly depressed regions of the vascular axis, while the laminar strands (lateral and median) mark the position of the four or five outward projecting points of that axis. These strands were not definitely determined in the earlier study (12) of *Quercus* seedlings, but more recent examination has demonstrated their occurrence both in *Quercus* and in *Carya*. It is thus apparent that the number of vascular bundles entering the stem at each node is much greater than commonly believed; the number varying with different foliar appendages in *Carya*, averages 17–18 for the second foliage leaf (fig. 5), 16 for the third, and 10–12 for the fourth and fifth (figs. 10, 11), with an appreciably smaller number of traces contributed by the scale leaves.

In *Carya*, as in *Quercus*, stem bundles may be distinguished in longitudinal sections of the epicotyl early in its development, in stages preceding leaf formation. But with the appearance of foliar appendages, so close is the succession of leaf primordia at the apex of the stem, and so reduced the extent of the apical meristematic region of the stem axis, that cauline strands no longer are distinguishable, and it is altogether probable that the apical meristem becomes from this time wholly occupied with the formation of primordia. Thus with the formation of leaves or leaflike appendages at the stem tip, all vascular strands of the primary vascular cylinder are "common" bundles, which enter the stem from the leaf base along a curved path, and afterwards differentiate longitudinally through two or three short internodes, sooner or later connecting laterally with procambial strands from earlier formed leaves.

Continued development within each leaflet involves further differentiation of the primary midrib, and marginal meristems, with the origin within the marginal meristems of other centers of lignification which differentiate basipetally to meet the primary and secondary laminar strands. Later intercalary meristematic growth in the pri-

mordial leaf leads to formation of a stalk between the blade and the leaf base.

Lignification of all vascular strands commences at the point of origin, in the case of the primary foliar strands with the procambial cells of the leaf base, and progresses with the advance of these elements inward toward the stem, and outward and upward toward the tip of the leaflets.

Scale leaves (bud scales)

The primary axis of seedlings, 3–8 weeks old, usually bears 6–8 scale leaves. These appendages, excepting those immediately preceding the first foliage leaves, are small, reddish brown, leathery bodies with a broad base which narrows gradually upward, and bears at the tip a rudimentary leaf lamina consisting of a median pointlet and two feebly developed lateral segments (figs. 15, 16). The sizes of such scales may with successive members show considerable variance; that of the oldest or first formed averaging 0.9–1.1 mm. in length, the second and third pairs 1.2–1.4 mm., while scale leaves immediately preceding the first foliage leaves often attain a length of 1.7–2.5 mm. The length of the first foliage leaf (possibly a transition type) may not exceed 3–4 mm. (inclusive of lamina, petiole, and base). Further, with successive bud scales there may be observed an increase in the size and prominence of the trilobed leaf lamina, that is, through the first four or six scales; the last formed scale leaf consists of a leaf base 0.5–0.6 mm. in width in adult condition, narrowing gradually to an elongated sharply pointed single-lobed lamina.

The vascular supply of each of the first two or three pairs of scales usually consists of three small laminar bundles, which in their basipetal development through the base of the appendage unite, and as a single strand connect with the primary cylinder (fig. 23). The later formed scale leaves may exhibit a more extensive vascular system, some 7–9 strands (fig. 17), which in their basipetal progression traverse the thickened median central region of the sheath of the appendage to that point in the base where the usual anastomosis occurs, reducing the 7–9 bundles to five. These five strands connect with the primary vascular axis at three points, three of the five form-

ing the median leaf trace, the fourth and fifth, as lateral strands, describing partial arcs through the leaf base to the lateral leaf gaps (fig. 22).

The primordia of the scale leaves appear in close succession at the growing point, and, as in the case of the foliage leaf primordium, each is first distinguishable as a small knoblike structure which by rapid meristematic growth soon extends as a ridge over and about the vegetative point. For a short time (varying in different scales) development of the laminar portion of the primordium parallels that of the foliage leaf. Shortly after the formation of the first 3 primary segments, dominant growth commences in the sheathing portion of the appendage, preventing further elaboration of the lamina.

The procambial elements of the primary laminar bundles are differentiated early in the embryonic base of the scale, one strand at the base of each of the three lobes of the laminar primordium. Longitudinal development of these strands is from their point of origin both acropetal and basipetal. The procambial elements identified with the lower section of the base of the foliage leaves are also found in the scale leaves, appearing concurrently with the origin of the median primary bundle of the blade and to either side of that bundle. Their longitudinal differentiation is chiefly in a basipetal direction.

Summary

1. The promeristem of the stem axes of seedlings of *Carya cordiformis* has its origin in three successive horizontal initial units, associated at the apex of the stem's axis in the form of an inverted cone or wedge.

2. Foliar organs formed by the main axis of seedlings 3–8 weeks old consist of 6–8 scale leaves, 5–6 foliage leaves, and primordia. The transition from scale to foliage appendage is from scale leaves exhibiting a marked, although reduced, laminate structure to uni-, tri-, and five-pinnate foliage leaves.

3. Variability in leaflet number, as well as an asymmetrical formation of leaflet primordia, occurs in the foliage leaves both of seedling and winter buds; in seedlings an increase from one to five leaflets with successive leaves, in winter buds an increase from seven to nine

leaflets in the first six leaves, but in later formed leaf primordia a decrease from seven to five leaflet primordia.

4. Lateral leaflet primordia in the foliar organs arise in acropetal succession, as successively developed lobes on the marginal meristems of the "upper leaf" of the primordium, with a reduced development of this portion of the primordium in the scale and first formed foliage leaves of seedlings.

5. Differentiation of the desmogen or procambial elements of the "primary" vascular bundles of the foliage leaf takes place early, and is first evident in that region of the primordium destined to become the upper section of the leaf base. The first strand appears while the primordium is in the unilobate condition, as a group of desmogen elements occupying a central position at the base of the median leaflet lobe. Other primary strands arise later, with the evolution of lateral pinnae, one beneath each of the lateral leaflet primordia. With continued meristematic activity in the basal section of each leaflet, primordium "secondary" desmogen strands arise to either side of the differentiating primary strands. Longitudinal development of these several groups of strands (both primary and secondary) is from their point of origin both acropetal and basipetal.

6. Concurrent with the origin of the primary bundles of the lamina is the differentiation of a set of vascular strands deep within the primordial leaf base. These strands (5–9 in number) differentiate acropetally only to a point of union with the primary laminar bundles. Basipetally they maintain a direct and independent course, entering the primary vascular axis to either side of the median laminar strands. Within the primary cylinder they occupy the slightly depressed regions of the vascular axis, while the laminar strands (lateral and median) mark the position of the outward protecting points or ridges of that axis. Such vascular elements, heretofore confused with and described as "cauline" bundles, account for the closely reticulate character of the primary vascular cylinder of woody forms like *Carya* and *Quercus*.

7. Cauline strands are distinguishable as units of the primary vascular axis of the epicotyl only through that embryonic period which precedes leaf formation.

Grateful acknowledgment is made for helpful criticism given by Professor W. J. G. LAND during the progress of this study.

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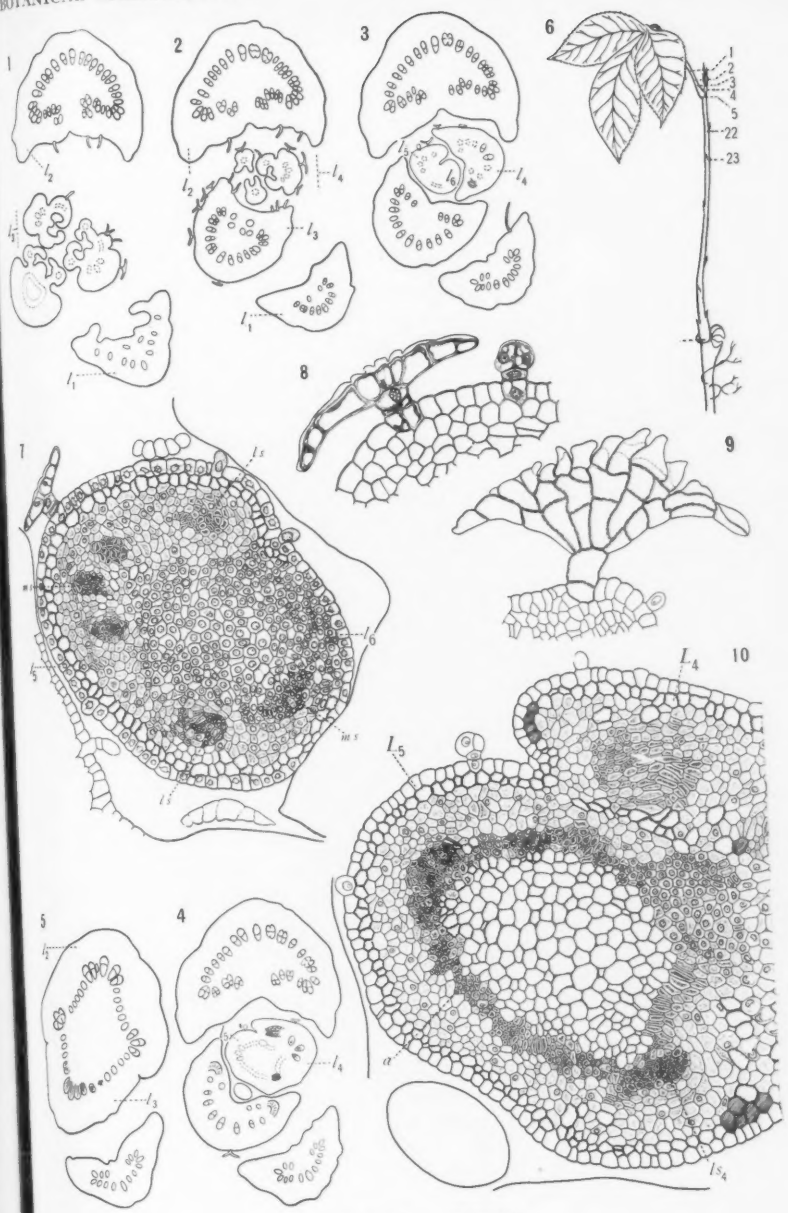
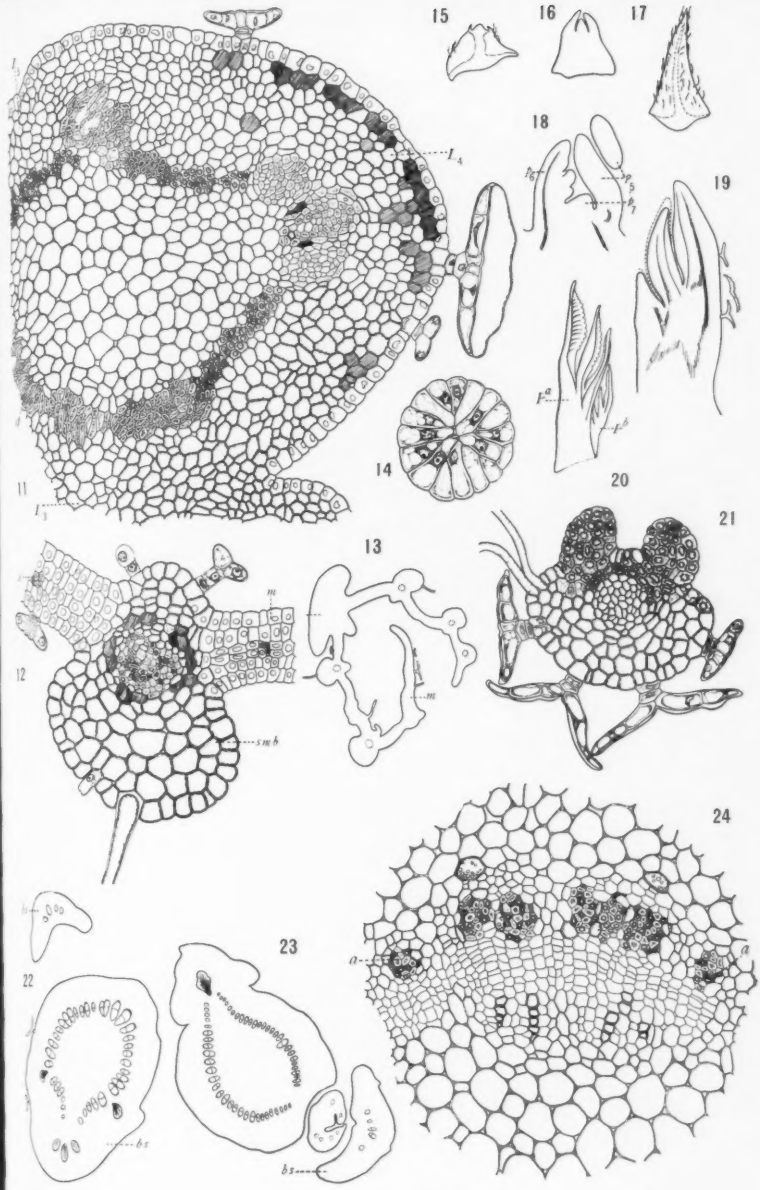


LANGDON on CARYA



LANGDON on CARYA

EXPLANATION OF PLATES I, II

With the exception of figs. 27 and 28, all illustrations are of *Carya cordiformis* seedlings.

PLATE I

FIGS. 1–5.—Sections at successive levels through terminal bud of 5-weeks-old seedling. L_1–L_6, first to sixth leaves in order of development; ×27.

FIG. 6.—Eight-weeks-old seedling, lettering and figures indicate approximate positions in bud of figs. 1–5; ×0.6.

FIG. 7.—Detail of terminal portion of bud 24 μ below that of fig. 3; three median "primary" strands of fifth leaf seen drawing toward center; left and right lateral primary strands of same primordium likewise differentiating toward stem axis; first formed primary strand (*ms*) of sixth or youngest foliar primordium definitely outlined; ×226.

FIG. 8.—Detail of glandular hair from ventral surface of leaflet primordium; ×320.

FIG. 9.—Glandular hair from ventral surface of mature leaflet; ×267.

FIG. 10.—Detail of stem axis and basal part of fifth primordium, 48μ below section illustrated in fig. 7; desmogen between median and lateral primary strands of second youngest primordium (L_5) clearly defined but as yet unorganized; these strands with median and lateral laminar bundles of fifth and sixth primordia now part of primary vascular cylinder, with median and lateral foliar strands occupying the points of that cylinder, the later differentiated basal desmogen the depressions; ×228.

PLATE II

FIG. 11.—Detail of basal portion of fourth leaf at point of union with stem axis; desmogen of fifth leaf to upper left side; centermost of three median strands of fourth leaf shows differentiation into primary xylem and phloem regions; left lateral of fifth primordium connects with primary cylinder; median strand of sixth primordium inserted on lower lateral of fourth leaf; ×226.

FIG. 12.—Detail of one of secondary ribs (*smb*) with adjacent blade meristems (*m*), same as outlined in fig. 13 (note prominent protective hairs as outgrowths from dorsal surface of leaflet); colleters either on dorsal or ventral face of pinna; ×267.

FIG. 13.—Transverse section of nearly mature leaflet showing primary midrib and conduplicate blade with secondary ribs; ×32.

FIG. 14.—Dorsal view of one of disk-shaped mucilage secreting glands; ×534.

FIGS. 15–17.—Successively formed scale leaves, showing increase in size and prominence of trilobed lamina with successive scales; ×9.

FIG. 18.—Median long section through apex of primary axis of an 8-weeks-old seedling, showing primordia of three foliar organs; ×53.

FIG. 19.—Longitudinal section through young foliage leaf, with lateral and median leaflets showing differentiation into midrib and marginal meristems; as

yet no indication of origin of marginal teeth from lateral meristems of each leaflet; ×53.

FIG. 20.—Foliage leaf primordia (P^A and P^B) dissected from seedling bud; ×9.

FIG. 21.—Detail of tip portion of leaflet showing differentiating primary midrib (*pmb*) with dorsal colleters, also ventral ridges of meristem (*m*) from which blade is formed; ×267.

FIG. 22.—Transverse section of seedling stem showing connection of one of later formed scale leaves with stem axis; section through upper part of node; ×32.

FIG. 23.—Transverse section of stem showing vascular connection of early formed scale leaves with stem axis; ×32.

FIG. 24.—Detail of group of foliar bundles at point of union with primary vascular axis; ×267.

COMPARATIVE STUDY OF RIVER BLUFF SUCCESSION ON THE IOWA AND NEBRASKA SIDES OF THE MISSOURI RIVER

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 415

DAVID F. COSTELLO

(WITH SEVEN FIGURES)

Introduction

A contrast in appearance of river bluffs on opposite sides of the Missouri River near Nebraska City, Nebraska, was the occasion for a comparative study of plant succession on these east- and west-facing slopes. When viewed from a distance the impression is given that trees are almost entirely absent from the west-facing Iowa bluffs. They are characterized by a very rugged topography, much dissected by erosion, and a bareness that comes of the clay soil of which they are composed (fig. 1). The east-facing Nebraska bluffs appear to be more regular in outline, with fewer dissections, and practically no promontories, and to be well covered with forest vegetation (fig. 2).

In this preliminary study, observations were confined to an area about 15 miles square. On the Iowa side, studies were made on the bluffs for a distance of approximately 15 miles north of Hamburg, Iowa, which is near the Iowa-Missouri state boundary. On the Nebraska side, observations were made on all the bluffs for a distance of 5 miles north of Nebraska City and to a point 10 miles south of that city. Thus the areas observed on different sides of the river were almost directly opposite each other. The width of the flood-plain between the bluffs at this point is approximately 10 miles. Studies were limited almost entirely to the river-facing bluffs.

The order of procedure was first to determine as nearly as possible the usual order of succession, or successions, on the river bluffs. With this as a background, study was then directed so as to determine the differences, if any, that existed between the successions on

bluffs on opposite sides of the river. Steps were then taken to find an explanation for the phenomena.

FIGS. 1, 2.—Fig. 1 (above), west-facing treeless bluffs on Iowa side of Missouri River; fig. 2 (below), east-facing forest-covered bluffs on Nebraska side.

Plant succession

The plant associations of the Missouri River bluffs have been variously described by different investigators. POUND and CLEMENTS (7) for Nebraska, in considering the river bluff formation, speak of the red oak-hickory association, the bur oak-elm-walnut association, and the linden-cedar-ironwood association. POOL, WEAVER, and JEAN (6) describe the "communities of the region about Peru in the

order of their place in succession as the bur oak-yellow oak type, the black oak-hickory type, the red oak type, and the linden-ironwood type." In actual practice it is impossible to describe the associations of any limited area of the bluffs by means of a general formula, because conditions of habitat permit the invasion of other species, or exclude certain of those which are characteristic of the associations, so as to make the type both variable and heterogeneous. For purposes of comparison, it has been found best to use a succession in which replacement takes place in the following order: bare soil, grassland, shrub association, bur oak-yellow oak association, red oak-black oak-hickory association, elm-ash-walnut association, linden-ironwood association. An elm-ash-ironwood association is prominent in some places and frequently takes the place of the elm-ash-walnut group. In this study, where observations were confined almost entirely to the river-facing bluffs, even these types failed in some instances.

Bare soil

In the Missouri River bluff region, the only natural agency that can produce a bare surface, devoid of vegetation and of disseminules for the propagation of plants, is erosion. Considerable erosion in these bluffs has come as the direct result of river action. In meandering over its floodplain, the Missouri River has cut hard on one bank and then on the other, producing high bluffs that were almost vertical at the time of their formation. At the present time, although the river is cutting hard on its right bank, little erosion is taking place at the base of the bluffs owing to its action. With the exception of a strip north of Nebraska City, the river is confined entirely to cutting its floodplain in the area studied.

Erosion, due to running water, has contributed greatly to the present topography of the bluffs. River action, however, is the only means that produces a surface where plants are entirely absent. Soil that is exposed by the river has been covered so long that any seed that could possibly still be present has long since lost its viability; hence the only means by which these areas are populated is through the agencies of plant distribution.

GRASSLAND ASSOCIATION

The possibility of fixing any plant as an absolute pioneer on these clay surfaces is remote. Conditions are not exacting enough to limit the number of plants that may serve as pioneers, while slump action

FIGS. 3, 4.—Fig. 3 (above), Iowa bluff showing typical grassland; floodplain of Missouri River in upper left; fig 4 (below), transition from grassland to shrub and timber associations on Iowa bluffs.

may introduce species that are entirely foreign to the situation. It is by this means that the great majority of eroding bluffs are finally "captured." The type that follows "capture" may well be classified as grassland, since grasses predominate in number of individuals so as to give character to the landscape (fig. 3). The usual pioneers that introduce this type are *Taraxacum officinale*, *Melilotus alba*, *M.*

officinalis, *Aquilegia canadensis*, *Verbascum thapsus*, and *Rumex crispa*. Later *Stipa comata*, *Glycyrrhiza lepidota*, *Petalostemum purpureum*, *P. multiflorum*, *Yucca glauca*, *Cirsium* sp., and *Liatris squarrosa* make their appearance, and a typical prairie flora results.

Shrub association

It is here that the transition from prairie grassland to timberland takes place. The association is usually found at the crest of the bluffs and bordering many of the patches of timber that are found on the more protected slopes (fig. 4). Many of the ravines in the prairie grassland association are given over to a shrub association. This is characterized by a low growth of woody forms, and may vary from an open stand of sumac on the prairie to a thick impenetrable tangle of woody forms in the gulches that have been formed by erosion. The more prominent species are *Rhus typhina*, *R. glabra*, *Cornus asperifolia*, *Prunus americana*, and *Crataegus* sp. Not all of these species are found in one place by any means; more frequently a single species is dominant within the limits of any particular area.

Bur oak-yellow oak association

This is the association that usually encroaches upon the prairie, either with or without the aid of the shrubby forms. The growth is open and frequently the trees do not touch, so that the characteristic growth form is a tree with a comparatively low spreading and well rounded crown. *Quercus macrocarpa* and *Q. muhlenbergii* are the dominant species. The undergrowth normally consists of a layer of shrubby forms, such as *Corylus americana*, *Symphoriocarpos symphoriocarpos*, *Prunus americana*, *P. virginiana*, *Rhus glabra*, and *Cornus asperifolia*. When the canopy is less open the undergrowth may change to one in which *Ribes gracile*, *R. occidentalis*, *Psedera quinquefolia*, *Rhus toxicodendron*, *Vitis vulpina*, and *Smilax hispida* are dominant. The herbaceous layer is variable, and may consist of grasses such as *Andropogon scoparius* and *A. furcatus*, in combination with *Oenothera laciniata*, *Monarda fistulosa*, and various species of *Solidago;* or it may be practically devoid of herbaceous species if the shrub formation above is dense enough.

Bur oak-black oak-hickory association

This association is made variable by a considerable number of intruders that frequently appear. *Quercus macrocarpa*, *Q. velutina*, and *Carya ovata* give character to the association. It is not at all uncommon, however, to find specimens of *Q. rubra*, *Fraxinus americana*, *Juglans nigra*, *Carya porcina*, *Celtis occidentalis*, *Gymnocladus dioica*, *Ostrya virginiana*, *Cercis canadensis*, and *Juniperus virginiana*. The most important lianas are *Smilax hispida*, *Vitis vulpina*, and *Psedera quinquefolia*. Other climbers occur, principally in the secondary layer, such as *Clematis pitcheri* and *Echinocystis lobata*. The secondary layer nearly always consists of seedlings of the type that makes up the association. Shrubs are not numerous as a rule, and when they do occur it is usually as a result of some disturbance of the surrounding vegetation. The herbaceous layer is represented by such forms as *Viola* spp., *Aquilegia canadensis*, *Claytonia virginica*, *Phlox divaricata*, *Erythronium albidum*, *E. americanum*, and *Erigeron philadelphicus*. With the disappearance of these forms and the advent of drier conditions, the flora changes to one in which *Verbascum virgatum*, *Helianthus annuus*, *Abutilon theophrasti*, *Dentaria* sp., *Cryptotaenia canadensis*, *Osmorrhiza longistylis*, *Cassia chamaecrista*, *Sanicula marylandica*, *Mentha piperita*, and *Eupatorium maculatum* are prominent.

Elm-ash-walnut association

This association is even more variable than any that has yet been described. The dominant trees are *Ulmus fulva*, *Fraxinus americana*, and *Juglans nigra*. As in the preceding group, *Celtis occidentalis*, *Gymnocladus dioica*, *Ostrya virginiana*, and *Juniperus virginiana* may appear. Specimens of hickory are rarely found and oaks are also infrequent. *Staphylea trifolia*, *Amelanchier canadensis*, and *Tilia americana* make their appearance in the more mesophytic localities. *Prunus serotina* is frequently found in this admixture although it may occur in the preceding association.

Linden-ironwood association

This is the climax forest of the bluff region. The characteristic species are *Tilia americana*, *Ostrya virginiana*, *Fraxinus pennsyl-*

vanica, and *Morus rubra*. Frequently the last two species are entirely absent. The formation is characterized by tall straight trees with compact close fitting tops that provide a deep shade. A secondary layer of small trees and shrubs may or may not be preent. When it is preesent it usually consists of seedlings of *Tilia americana* and *Ostrya virginica* in combination with *Cornus stolonifera*, *C. asperifolia*, *Rhamnus lanceolata*, and *Symphoriocarpos symphoriocarpos*. *Rhus toxicodendron*, *Psedera quinquefolia*, *Smilax hispida*, and *Clematis virginiana* occur abundantly. The mesophytism of the situation is revealed by the presence of such forms as *Impatiens biflora*, *Claytonia virginica*, *Smilacina racemosa*, *Polygonatum biflorum*, *Galium aparine*, *Sanguinaria canadensis*, *Orchis spectabilis*, *Podophyllum peltatum*, and *Adiantum pedatum*. The linden-ironwood association is found at its highest development only in sheltered ravines at the base of the bluffs.

Bluff successions compared

The foregoing description has been given to provide a basis for the comparison of the bluff associations and their succession on opposite sides of the river. Points of difference and of similarity were brought out by observations, and measurements taken systematically and at random in the various associations. An exhaustive experimental study requiring considerable time will be necessary before the complete set of factors responsible for the differences can be determined.

Rate of succession

In considering data that have been brought out by a study of the comparative areas of grassland and of timberland on the two sides of the river, it is apparent that the rate of succession is much faster on the Nebraska side. Within equal periods of time a much greater amount of bluffland has become forested on the Nebraska side of the river than on the Iowa side. (This statement is made with respect to the river-facing bluffs only.) Protected bluffs and sheltered ravines behind the first range of bluffs bordering the floodplain show stages of vegetation as far advanced as those on the Nebraska side. Thus there is no doubt as to the possibility of reaching the climax of the area on the Iowa side.

An index of the rate at which succession takes place on opposite

sides of the river is provided by the secondary successions observable at various places. All of these seem to indicate that any disturbance of the natural vegetation remains visible longer on the west-facing than on the east-facing slopes.

Number of individuals and variety of species

By means of belt transects 8 m. wide and quadrats 10 m. square it was found that the Nebraska bluffs excel both in number of species of trees and in number of individuals. The greater number of species is brought about by the appearance of intruders in the associations common to both sides of the river. Some of these invading species have already been mentioned in the description of the associations.

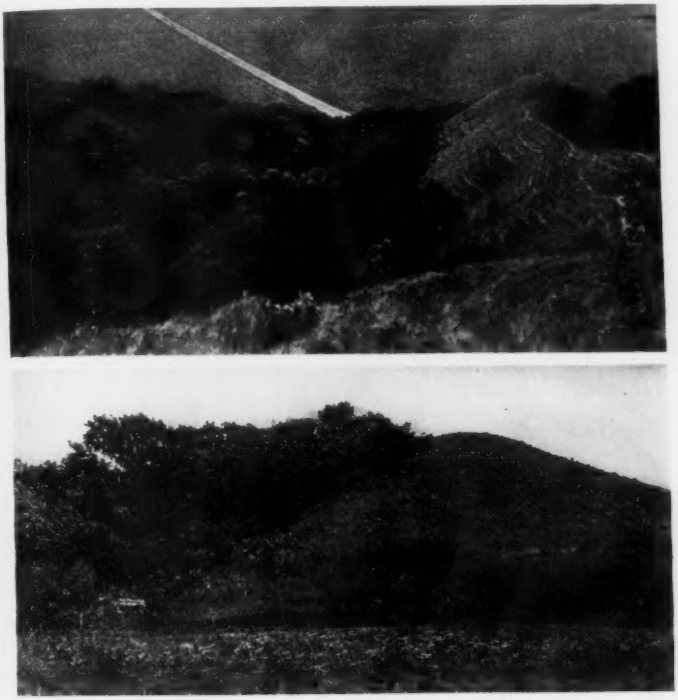
A comparison of undergrowth in the various woodlands would seem to indicate that there is a difference in density and number of species, but it is possible that grazing and biotic disturbances have rendered such data unreliable.

Position on bluffs

It has been determined that corresponding associations are higher on the Nebraska bluffs than on the Iowa bluffs. In many cases the bur oak-yellow oak association, which has reached the crest of the east-facing bluffs, is to be found only half way up the slope on west-facing bluffs (fig. 5). In other situations it is confined entirely to the ravines or to the sheltered gulches on west-facing bluffs. In progressing down the bluff, the whole range of associations may be passed through until the linden-ironwood association is reached at the bottom. More frequently, however, where the bur oak formation is found only part way up the bluff, the base of the bluff is reached before the linden-ironwood association is encountered; conditions have not reached the mesophytism that will support such a forest.

A noteworthy feature of the Iowa bluffs is the telescoping of associations. Within a comparatively short distance all of the woodland associations may be encountered. The change from the bur oak-yellow oak association to the linden-ironwood climax has been observed within a space of 30 m., making a separation of associations

into distinct units an impossibility. This indicates a quick change from the mesophytic to the xerophytic, a phenomenon which is not nearly so evident on any of the Nebraska bluffs.



FIGS. 5, 7.—Fig. 5 (above), forest at crest of bluff on east-facing slope, half way up west-facing bluff (wind blows from left to right); fig 7 (below), Iowa bluff with forest growing in area protected from prevailing winds (wind blows from right to left).

COMPARISON OF LINDEN-IRONWOOD CLIMAX AREAS

As a result of measurements of area and a tabulation of species, taken systematically and at random, it has been found that a greater area has reached the linden-ironwood climax on the Nebraska side than on the Iowa side. Incidentally this is an indication that the rate of change is greater on east-facing than on west-facing slopes.

It is interesting to note that where the bluffs take an east and

west trend at one point on the Iowa side, thus providing a north-facing slope next to the floodplain, development of vegetation is much the same as that on the Nebraska side of the river. The significance of this will be seen when the cause of the difference in rate of succession on the two opposing sets of bluffs is taken into consideration.

Treelessness of west-facing bluffs

It is doubtful whether any one factor could be important enough to cause such a striking difference in appearance in two series of

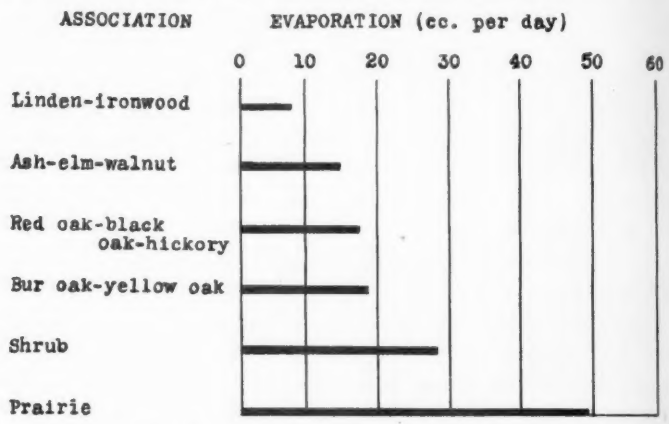


Fig. 6.—Average daily evaporation from atmometers in various associations on Missouri River bluffs.

bluffs such as have just been described. On the other hand, it seems probable that one factor has been responsible to an extent greater than that of all other factors combined in bringing about the vegetational complex that now exists on the slopes of the Iowa and Nebraska river bluffs. That factor is evaporation, caused by the prevailing winds.

In the region studied, the prevailing winds from April 1 to October 1 are from the south and southwest, and from October 1 to April 1 from the northwest. East-facing slopes are protected from the drying influence of these winds, while west- and southwest-facing slopes are windswept at all seasons of the year. Atmometer readings (fig.

6), taken from standardized spherical atmometer cups devised by LIVINGSTON (4), show that the rate of evaporation is almost twice as great on west-facing slopes where the wind strikes, as on east-facing slopes where protection is afforded. The amount of evaporation increases as one passes from the linden-ironwood association toward the bur oak-yellow oak association. When the shrub and grassland associations are reached the rate is almost twice that of the bur oak association, and nearly six times that of the linden-ironwood association. Rates of evaporation in similar associations on opposite sides of the river were nearly the same.

Further evidence in support of the evaporation theory is furnished by the observation that almost without exception, on both the Nebraska and the Iowa sides of the river, woodland vegetation ceases abruptly when the crest of the bluffs is reached. The change from forest to prairie or to shrub associations, when present, is so sharp that it is almost diagrammatic (fig. 7). In every case the east-facing slopes are covered with woodland while the west-facing slopes are bare of trees.

Still further evidence in support of this idea was brought out by the observation that apparent exceptions to the rule, west-facing bluffs covered with timberland, were protected by other bluffs to the windward. It would appear, therefore, that the explanation of the treelessness of west-facing bluffs in general is due, directly or indirectly, to the effects of a high rate of evaporation, caused by the prevailing winds during the growing season.

FUTURE STUDIES

The writer hopes to make a thorough and systematic study of all the factors at play in the bluff region described. The work of previous investigators has indicated the method of procedure. LIVINGSTON (5) has shown that there is a correlation between the evaporating power of the air and the growth of plants during the months in which frost is absent. WEAVER (9) believes that differing rates of evaporation in various plant formations are important factors in causing plant succession. FULLER (2), studying environmental factors on the sand dunes in northern Indiana, states that "differences in the rates of evaporation in the various plant associations studied

are sufficient to indicate that the atmospheric conditions are efficient factors in causing succession." It would seem worth while, therefore, to make careful measurements of atmospheric conditions over a wide area on the Iowa bluffs, in order to determine whether plant succession might be retarded or even made impossible in the presence of a high rate of evaporation.

Further studies will be necessary for a complete explanation of the treelessness of the Iowa bluffs. WARMING (8) states that "the absence of trees from many places on the earth is mainly due to wind," but does not go into detail. WEAVER and CLEMENTS (10) mention the retarding effects of increased transpiration on trees and further state that the drying effect of wind may result in the death of trees. BRYAN (1) suggests a point of attack through a study of the relation of the various associations to ground water level. It is possible that lowering of the water table, due to ravine cutting, has made it difficult for trees to grow on the west-facing slopes. This in turn calls attention to the great amount of erosion that has taken place on the west-facing slopes. GEIGER (3) has found that slopes facing the wind get more precipitation per unit of surface than slopes turned away from the wind. It is possible then that the prevailing winds have acted directly, through increasing the evaporation rate, and indirectly through influencing the topography over centuries, in producing treeless slopes on the west-facing bluffs of the Missouri River.

Summary

1. Study of the river-facing bluffs of the Missouri River was undertaken to gain a more accurate concept of the differences that appear to exist between the opposing bluffs.

2. In order to provide a basis for discussion, a brief description of the order of succession on these river bluffs and their plant associations is given.

3. The order of succession was found to be the same on opposite sides of the river.

4. The rate of succession is faster on east-facing bluffs.

5. East-facing bluffs excel both in number of individuals and in variety of species.

6. Corresponding associations are found higher on east-facing than on west-facing bluffs.

7. A greater area is occupied by the linden-ironwood climax on east-facing bluffs than on west-facing bluffs.

8. These differences, as well as the treelessness of west-facing bluffs, appear to result from the high rate of evaporation caused by prevailing winds during the growing season.

9. It is hoped to study in detail the environmental factors in the various plant formations and associations on the Missouri River bluffs.

The writer is grateful to Professors H. C. COWLES and G. D. FULLER of the University of Chicago for encouragement and criticism during the progress of this investigation.

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NEW OR OTHERWISE NOTEWORTHY COMPOSITAE. VI

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 418

EARL EDWARD SHERFF

Bidens mildbraedii sp. nov.—Herba perennis e radice lignescenti, erecta, probabiliter 7–12 dm. alta, ramis fastigiato-erectis, caule ramisque atropurpureis, glabris, angulato-teretibus vel subtetragonis. Folia opposita, petiolo adjecto 0.7–1.7 dm. longa, nunc indivisa, linearia, 2–7 mm. lata, superne ad apicem acerrimum sensim elongato-attenuata inferne in petiolum marginatum 2–3.5 cm. longum angustata; nunc supra petiolum utrinque anguste 1-lobata lobo tenuiter lineari 1–3 cm. longo et 0.5–2 mm. lato; nunc pinnatim 3- vel 5-partita, foliolis linearibus 1–4 mm. latis, inferioribus interne saepe rursus 1-lobatis, petiolo tenui 2–4 cm. longo; laminis segmentisve membranaceis, supra glabris infra glabris vel aegre adpresso-hispidis, marginaliter parce subrevolutis sed hispido-ciliatis. Capitula corymbosa, tenuiter pedunculata pedunculis superne dense pilosis pilis patentibus, radiata, pansa ad anthesin circ. 2.8–3.4 cm. lata et 8–12 mm. alta. Involucri bracteae inferne valde superne aegre hispidae, exteriores 8–10, lineari-oblongae, apice indurato-nitidae et saepius obtusae, 6–14 mm. longae; interiores ovatae, 6–9 mm. longae. Flores ligulati circ. 8, sicci atroflavi, lineari-oblongi, circ. 1–1.3 cm. longi et circ. 2–3.5 mm. lati, apice profunde acriterque lobulati lobulis 1–3 mm. longis. Paleae lineari-oblongae, subtiles, apice obtusae, demum 7–9 mm. longae et circ. 1 mm. latae. Achaenia lineari-oblonga, plana, brunneo-atra, unaquaque facierum circ. 8-sulcata, faciebus marginibusque erecto-hispida, nunc parva, corpore 4.5–6 mm. longa et circ. 0.6–0.8 mm. lata, apice valde erecto-setosa et biaristata aristis erectis vel suberectis basaliter sursum hispidis aliter nudis 0.8–1.3 mm. longis; nunc majora, corpore 7–9 mm. longa et 1–1.6 mm. lata, apice subsetosa et biaristata aristis patentibus inaequaliter 0.5–1 mm. longis, nudis vel basaliter rarius erecto-setosis.

Specimens examined: *Mildbraed* 9777, alt. about 1000 m., Buar, Kamerun, July, 1914 (type in Herb. Kew); *idem* 9386, *eodem loco*, May, 1914 (Herb. Kew).

The two sheets examined are of material collected two months apart. The first sheet has two plants. These were collected in May. One has a sterile, leafy stem about 2.7 dm. tall; the other has a sterile stem about 2.4 dm. tall and a fertile stem about 6.2 dm. tall, bearing three fruiting heads. The leaves are of the more compound type and offer a strong superficial resemblance to those of the North American *Coreopsis delphinifolia* Lam. The exterior involucral bracts are equal to or a fourth or third shorter than the interior ones. The achenes are the larger ones of the Latin description.

The second or type sheet bears material of a much better developed plant (or plants). This was collected in July. About two dozen heads are present. The leaves are simple or laterally 2-lobed. The exterior involucral bracts tend greatly to exceed the interior ones. The achenes are the smaller ones of the Latin description.

As these differences appear to be of a seasonal nature, it seems inadvisable to attempt any varietal distinction of one form from the other.[1]

Bidens rhodesiana sp. nov.—Herba erecta, perennis, ramosa, verisimiliter circ. 8–10 dm. alta, breviter denseque hispida, caule ramisque tetragonis, internodiis elongatis. Folia opposita subsessilia vel petiolata petiolis alatis usque ad circ. 1.3 cm. longis, petiolo adjecto 3–7 cm. longa (inferiora non visa), membranacea sed rigidula, circumambitu nunc late nunc anguste deltoideo-ovata, pinnata, foliolis lateralibus 1–2 jugis ovatis terminali ovato lanceolatove, omnibus dentatis dentibus obtusis vel etiam orbiculatis sed acriter mucronulatis. Capitula pauca, longe tenuiterque pedunculata, radiata, pansa ad anthesin 5–6 cm. lata et circ. 1–1.2 cm. alta. Involucri bracteae dorsaliter hispidae exteriores circ. 8, nunc linearioblongae nunc etiam oblongo-ovatae, apicaliter obtusae, circ. 4–8 mm. longae; interiores ovato-lanceolatae 9–12 mm. longae. Flores ligulati circ. 9, flavi, ligula oblongo-oblanceolati, apice obscure 3-denticulati, 2–2.5 cm. longi. Paleae lineari-oblongae, circ. 7–8 mm. longae. Achaenia plana, atro-brunnea, lineari-oblonga, basim ver-

[1] I am greatly indebted to Dr. Arthur W. Hill, Director of the Royal Botanical Garden of Kew, for sending me the *Mildbraed* specimens for study.

sus paulo angustata, faciebus glabra, unaquaque facierum circ. 8-sulcata, marginibus sursum setosa, apice sursum setosa ac biaristata aristis tenuibus glabris plerumque 1–1.5 mm. longis.

Specimens examined: *A. J. Teague* 226, in the Odzani River Valley, District of Manica, Division of Umtali, Southern Rhodesia, 1914 (type in Herb. Kew).

Through some of its leaves this species approaches closely *B. ukambensis* S. L. Moore. From that species it differs easily, however, in its much broader flowering heads, smooth-faced biaristate achenes, etc.

Bidens setigeroides sp. nov.—Herba annua, erecta, laxe hispida, caule subtetragona, ramosa ramis suberectis, 3–9 dm. alta. Folia 2–3-pinnatisecta, breviter petiolata petiolis latis usque ad 1 cm. longis, petiolo adjecto usque ad circ. 7 cm. longa, segmentis membranaceis, acriter apiculatis et interdum in setas breves desinentibus, plerumque 1–2 mm. latis. Capitula subcorymboidea, tenuissime pedicellata pedicellis pubescentibus 2–6 cm. longis, numerosa, radiata, pansa ad anthesin $\pm$1.2 cm. lata et circ. 6 mm. alta, demum circ. 8–9 mm. diametro. Involucri bracteae plus minusve hispidae, exteriores plerumque 6, anguste lineares vel lineari-spathulatae, apicaliter obtusae, 2–3 mm. longae; interiores oblongo-ovatae, $\pm$3.5 mm. longae. Flores ligulati circ. 6, flavi, ligula oblongo-ovati, apice circ. 3-dentati, circ. 5–6 mm. longi. Paleae nitidae, glabrae, oblongae, subobtusae, apicem versus aurantiacae, 3–6 mm. longae. Achaenia oblanceolato-linearia vel late oblanceolata, nigra, exalata, non manifeste sulcata, dorso convexa ac glabrata, ventre plana vel concava ac costa mediana erecte setosa, marginibus crassis erecte ciliata, apice truncato exaristata sed erecte setosa, 2.2–3.5 mm. longa et 0.5–1.2 mm. lata.

Specimens examined: *Mr. J. D. Snowden* 411, growing 1–3 feet high in short-grassland at altitude of 5000 feet, Wallasi, Bukedi, Uganda Protectorate, British East Africa, October 17, 1916 (Kew).

Differs from *Bidens setigera* of Abyssinia and Eritrea in the less setigerous foliar teeth, the fewer exterior bracts of the involucres, the exaristate, smoother achenes, etc. It approaches in general appearance the habitally similar *Coreopsis negriana* Sherff of Galla-

land, but differs from that species in the smaller flowering heads, the setose, exalate achenes, etc.

BIDENS DIELSII **medusoides** var. nov.—A specie involucri bracteis exterioribus 14–20 (plerumque circ. 16–18), lineari-subulatis, 0.8–1 (rarius usque ad 2) cm. longis, inferne 0.6–1 (raro usque ad 1.5) mm. latis differt.

Specimens examined: *T. D. Maitland* 1004, frequent in grassland at altitude of 5000 feet, Wasa, region of Mt. Ruwenzori, Tropical East Africa, Dec. 15, 1925 (Kew).

In the young heads (much before anthesis) the exterior bracts are twice as long as the disk, with a resulting fanciful resemblance of these heads to the *medusa* stage of many of the Coelentera in the animal kingdom.

BIDENS SETIGERA **lobata** var. nov.—Folia circumambitu oblongo-lanceolata vel anguste deltoideo-lanceolata, pinnatim plus minusve incisa vel etiam subtripartita, inferiora non visa alia 2–5 cm. longa, dentibus perspicue setigeris.

Specimens examined: Cultivated in garden of *J. Veitch and Sons*, 1908, from material collected by *Captain Diespecker* in British East Africa (Kew, 2 sheets).

The first type sheet has the six flowering heads measuring about 2.2–2.7 cm. across, with about 12–16 exterior bracts. The second type sheet has likewise six flowering heads, but these are mostly 4–4.5 cm. across and the exterior bracts number 16–22. These differences are construed as representing different states of luxuriance due to conditions of cultivation. The difference in general aspect due to the different amounts of foliar dissection is great, but such a difference is known in many other species of *Bidens* and does not appear to justify specific segregation.

Bidens skottsbergii sp. nov.—Frutex glaberrimus, verisimiliter 1 m. altus, ramosus. Folia opposita, tenuiter petiolata petiolis circ. 1–3 cm. longis, petiolo adjecto 8–13 cm. longa, pallidiora, membranacea, indivisa, oblongo-ovata, subgrosseserrata (unico latere saepius 12–18-serrata), apice subobtusa, basi late cuneata, principalia 3.5–5 cm. lata. Capitula pauca, laxe paniculata, pedunculata pedunculo subtenui usque ad 9 cm. longo, radiata, pansa ad anthesin 3–4 cm. lata et 9–12 mm. alta. Involucri bracteae exteriores circ. 8–10, glaberri-

mae, nunc late lineari-oblongae nunc oblongo-spathulatae, apicaliter obtusae, demum saepe patentes, 4–6 mm. longae; interiores oblongo-lanceolatae paulo longiores, apicaliter pubescentes. Flores ligulati circ. 8, flavi, ligula nunc oblongi nunc obovati, apice truncato 2–5-dentati et saepe subprofunde scissi, 1.7–2 cm. longi et 6–8 mm. lati. Achaenia nigra, plana, lineari-oblonga, unaquaque facierum plus minusve 8-striata, corpore glabro 8–10.5 mm. longa et circ. 1.35 mm. lata, lateribus marginata sed non vere alata, apice biaristata (aliter glabra) aristis subvalidis, stramineis brunneisve, retrorsum multi-hamosis, 1.5–2 mm. longis.

Specimens examined: *Carl Skottsberg* 2092, near Puna Road, south of Hilo, Isl. Hawaii, Sept. 30, 1926 (type in Herb. Bot. Gard. Göteborg).

Most closely related to *Bidens populifolia* Sherff (of the Island of Oahu), from which it differs in its oblong-ovate, basally wide-cuneate leaf blades, its broader, shorter, and more oblong achenes, these lacking erect apical setae between the aristae and having the aristae more densely and regularly retrorse-hamose.

Heterosperma nanum (Nutt.) comb. nov.; *Microdonta nana* Nutt., Trans. Amer. Phil. Soc. ser. II, **7**:370. 1841.—BENTHAM and HOOKER (Gen. Pl. **2**:384. 1876) noted this species ("ex specimine parvo et auctoris descriptione videtur *Heterospermi* species") but did not make a definite new combination.

Isostigma molfinianum sp. nov.—Herba perennis, basi fruticosa, erecta suberectave, glaberrima, circ. 1.5 dm. alta, inferne simplex ac valde foliosa internodiis plurime circ. 2–4 mm. longis, superne corymboideo-ramosa ramis erectis gracilibus angulatis. Folia subcoriacea, inferiora lineari-oblanceolata, apicaliter plerumque 2–3-furcata dentibus apicaliter mucronatis usque ad circ. 8 mm. longis, inferne sensim in petiolum saltem 1–2 cm. longum angustata, petiolo adjecto 2.5–4 cm. longa et (sub dentibus) circ. 2.5–3.5 mm. lata; superiora anguste oblongo-linearia, apicaliter plerumque 2–3-furcata dentibus parvis rarissime integra acutaque, basaliter aegre angustata. Capitula (±10 in unico specimine) corymboideo-paniculatim disposita, aegre radiata, pansa ad anthesin circ. 8–11 mm. alta et circ. 1.2–1.6 cm. lata. Involucri bracteae exteriores circ. 9 vel 10, lanceolatae, tergo hispidae, marginaliter albido-hyalinae, circ. 3–4 mm. longae et circ. 0.6–0.75 mm. latae, adpressae vel superne reflexae;

interiores late oblongo-lanceolatae, tergo glabratae, marginaliter brunneo-hylinae, paulo longiores. Flores ligulati forsitan 8–10, ligula (4–6 mm. longa) late lineari-oblongi, circ. 5–6-striati, apice saepe dentati, tubo circ. 2 mm. longo; stigmatibus capilliformibus ligulam manifeste superantibus; ovario plano obovato, faciebus brunneis glabrato, apice biaristata aristis tenuibus patentibus circ. 5 mm. longis basaliter subsursum hispidis aliter calvis. Paleae lineares, superne coloratae et saepe tortae, 5–7 mm. longae. Flores tubulosi cylindrico-urceolati, corolla (circ. 6 mm. longa) profunde (fere usque ad medium) 4-fidi, lobis elongate lineari-lanceolatis; antheris stigmatibusque valde exsertis. Achaenia matura deficientia; ovariis planis, anguste obovatis, brunneis, faciebus pilis adpressis suberectisque plus minusve hispidis, apice perspicue biaristatis; aristis tenuibus, patentibus, brunneis, 4–5.5 mm. longis, corollae tubum gracilem saltem duplo superantibus, basaliter aegre sursum hispidis aliter levibus vel apicem versus raro 1 vel 2 hamis retrorsum hamosis.

Specimens examined: *G. Bodenbender*, marshy place ("totoral") at Quebrada, Province of La Rioja, Argentina, February, 1896 (type in Herb. Gray).

This species was unknown to me at the time my revision of the genus *Isostigma* was published (Bot. Gaz. **81**:241–257. 1926). The type sheet bears two small specimens, each about 1.5 dm. tall. They are nearest to *Isostigma herzogii* Hassl., of which only the type, a fragment likewise about 1.5 dm. tall, is known to me. *I. molfinianum* differs in having the stems thicker below, much shorter internodes and consequently many more leaves, practically all the leaves (excepting only the bracts of the inflorescence) apically 2–3-furcate instead of entire, the ligules 4–6, not 9–11, mm. long, the anthers more conspicuously exserted (often suggesting an extra corolla), the disk corollas more deeply lobed (the narrow sinuses often reaching almost half-way down to the slender tube), the aristae of all the ovaries much longer (4–5.5 not 1.5–2 mm. long) and those of the disk corollas more than twice as long as the corolla tube (instead of barely equaling it), etc. The florets all are somewhat discolored with age, mostly appearing at present somewhat purplish-brown. One ligule, however, has a more yellow-brown color.

For the privilege of examining the type I am indebted to Dr. Ivan M. Johnston of Gray Herbarium. He had received it from

Sr. José Molfino, "one of the foremost botanists of Argentina." It is a pleasure to commemorate Sr. Molfino in the choice of a trivial name.

In a recent article (BOT. GAZ. **89**:371–373. 1930) I presented a key to and conspectus of all known South American species of *Coreopsis*. It has seemed desirable to publish at this time corresponding treatments for the known African species of that genus. Accordingly they are presented herewith. Authentic material of *Coreopsis aspilioides* Baker (Kew Bull. **1898**:153. 1898) and *C. chevalieri* O. Hoffm. & Muschl. (Bull. Soc. Bot. France 57, Mem. VIII. 118. 1910) has not been studied and hence those two species are omitted. All other published species excluded here are those which have been found properly referable elsewhere, particularly to *Bidens*.

Clavis plantarum africanarum Coreopsidis

a. Achaenia valde obcompressa, marginibus saepissime tenuia alatave
  b. Aristae achaeniorum filiformia ac quam corporibus breviora, vel deficientes
    c. Plantae annuae (vel verisimiliter annuae)
      d. Folia superne hispida
        e. Achaenia (alis inclusis) circ. 3 mm. lata..30. *C. oligoflora*
        e. Achaenia (alis inclusis) 4–5 mm. lata...31. *C. mattfeldii*
      d. Folia superne glabra vel glabrata
        e. Achaenia exaristata.....24. *C. negriana*
        e. Achaenia biaristata
          f. Foliorum caulinorum saepius 2–3-pinnatisectorum segmenta anguste linearia; capitulis pansa ad anthesin 2.5–5 cm. latis
            g. Foliorum segmenta plerumque circ. 1 mm. lata; involucro hispido.....29. *C. leptoglossa*
            g. Foliorum segmenta plerumque 2–4 mm. lata; involucro glabrato vel subglabrato...28. *C. feruloides*
          f. Foliorum 2-pinnatisectorum segmenta principalia oblongo-lanceolata; capitulis pansis ad anthesin 2.5–4 cm. latis...27. *C. prestinariaeformis* var. *incisa*

f. Foliorum caulinorum integrorum laminae vel 3–5-partitorum segmenta late linearia; capitulis pansa ad anthesin 5–7 cm. latis.....39. *C. borianiana*

f. Foliorum 3–5-lobatorum foliola ovata vel ovato-sublanceolata.....27. *C. prestinariaeformis*

c. Plantae perennes (vel verisimiliter perennes)

d. Foliorum principalium laminae vel segmenta lanceolata vel latiora

e. Foliorum segmenta dentata dentibus perspicue elongatis (saepe 1–1.5 cm. longis).....21. *C. mildbraedii*

e. Foliorum segmenta diversa

f. Foliorum dentes in setas elongatas desinentes.....11. *C. glaucescens*

f. Foliorum dentes non setigerae

g. Folia indivisa

h. Folia scabra, saepius 10–16 cm. longa; involucro hispido.....19. *C. scabrifolia*

h. Folia glabra, 1.5–5 cm. longa; involucro glabro.....9. *C. barteri*

g. Folia divisa

h. Achaenia exaristata

i. Folia plerumque pinnata vel pinnatifida segmentis principalibus saepius late oblongo-lanceolatis vel ovatis, inter se saepe propinquis, supra scaberulis subtus tomentellis

j. Caulis primo tomentellus mox glabratus.....15. *C. whytei*

j. Caulis perpetuo tomentellus.....13. *C. pinnatipartita*

i. Folia 2–3-pinnatisecta, foliolis vel segmentis principalibus saepius anguste oblongo-lanceolatis, glabris.....14. *C. lupulina*

h. Achaenia biaristata

i. Capitula pansa ad anthesin 5.5–9 cm. lata

j. Folia pubescentia.....29. *C. bella*

j. Folia faciebus glabra.....18. *C. togensis*

i. Capitula pansa ad anthesin usque ad 4 cm. lata
j. Folia molliter denseque pubescentia; achaeniis plumbeo-nigris minutis corpore tantum 3–4 mm. longis.....16. *C. neumannii*
j. Folia glabra vel subglabra
k. Pauca folia divisa.....9. *C. barleri*
k. Folia plerumque divisa
l. Involucrum hispidum....12. *C. oblonga*
l. Involucrum glabrum...10. *C. monticola*

d. Foliorum principalium laminae vel segmenta late vel anguste linearia
e. Foliorum dentes saepe in setas elongatas desinentes; lamina indivisa, usque ad 2 dm. longa et 4–10 mm. lata .....20. *C. bracteosa*
e. Foliorum dentes non setigerae
f. Folia inferiora 1–2 dm. longa; involucri bracteae exteriores circ. 12, lineari-subulatae, 1–1.5 cm. longae .....4. *C. camporum*
f. Folia inferiora raro 1 dm. longa
g. Frutices
h. Achaenia exaristata
i. Segmenta ultima 2–3 mm. lata.1. *C. elgonensis*
i. Segmenta ultima multo angustiora.....
.....2. *C. chippii*
h. Achaenia biaristata.....3. *C. scopulorum*
g. Herbae
h. Capitula pansa ad anthesin 4–8.5 cm. lata
i. Involucri bracteae exteriores elongatae, lateraliter lobatae; ligulis sulphureis.....
.....5. *C. ellenbeckii*
i. Involucri bracteae exteriores normales; ligulis aurantiacis.....17. *C. ochracea*
h. Capitula pansa ad anthesin circ. 2–2.5 cm. lata
i. Folia atro-viridia, segmentis plerumque 1.2–2.5 mm. latis.....6. *C. linearifloba*
i. Folia pallida, segmentis plerumque circ. 1 (raro 2) cm. latis.....7. *C. schimperi*

b. Aristae achaeniorum subulata
c. Herbae annuae
d. Involucri bracteae interiores glabrae....26. *C. prestinaria*
d. Involucri bracteae interiores pilis subplanis obtectae....
.....27. *C. prestinariaeformis et* var. *incisa*
c. Herbae perennes.....8. *C. macrantha*
a. Achaenia tantum moderate vel aegre obcompressa
b. Achaenia exaristata; foliis indivisis spathulato-oblanceolatis
.....23. *C. jacksonii*
b. Achaenia biaristata aristis lanceolato-subulatis; foliis bipinnatipartitis.....25. *C. pachyloma et* var. *inanis*

Conspectus plantarum africanarum Coreopsidis

1. C. ELGONENSIS Sherff, BOT. GAZ. **80**:374. 1925.—Uganda.

2. C. CHIPPII M.B.Moss, Kew Bull. **1929**:196. 1929.—Southern Sudan.

3. C. SCOPULORUM Sherff, *loc. cit.* **88**:302. 1929.—British East Africa.

4. C. CAMPORUM Hutch., Kew Bull. **1921**:381. 1921.—Northern Nigeria.

5. C. ELLENBECKII O. Hoffm., Engler Bot. Jahrb. **38**:205. 1906.—Eastern Abyssinia.

6. C. LINEARILOBA O. Hoffm., *loc. cit.* **30**:430. 1901.—Southwesternmost German East Africa.

7. C. SCHIMPERI O. Hoffm., *loc. cit.* **38**:205. 1906; *Microlecane abyssinica* f. *elongata* Vatke, Linnaea **39**:497. 1875.—Abyssinia.

8. C. MACRANTHA Schz. Bip. *in* Walpers Repert. **6**:163. 1846; *Verbesina macrantha* (Schz. Bip.) A. Rich. Tent. Fl. Abyssin. **1**:408. 1847; *Coreopsis macroptera* Schz. Bip. *in* Schweinf. Beitr. Fl. Aethiop. 284. 1867; *C. prestinaria* f. *elatior* Vatke, Linnaea **39**:498. 1875; *Prestinaria macrantha* Schz. Bip. *ex* O. & H. *in* Oliver Fl. Trop. Afr. **3**:391. 1877.—Abyssinia.

9. C. BARTERI O. & H. *in* Oliver Fl. Trop. Afr. **3**:390. 1877; *C. badia* Sherff, Bot. Gaz. **76**:90. 1923.—Northwestern Africa, from Kamerun west to Togo and northward to Borgu.

10. C. MONTICOLA (Hook. f.) O. & H. *loc. cit.*; *Verbesina* (*Prestinaria*) *monticola* Hook. *f.*, Jour. Linn. Soc. **7**:200. 1864.—Kamerun.

A pilose variety of this species exists and has been recognized in herbaria by OTTO HOFFMANN, HUTCHINSON and DALZIEL, and others.

11. C. GLAUCESCENS O. & H. *loc. cit.* 389; *C. abyssinica* f. *latisecta* Vatke, Linnaea **39**:499. 1875 (*nomen subnudum*).—Abyssinia.

12. C. OBLONGA Sherff, BOT. GAZ. **76**:80. 1923.—Lake Tanganyika region, eastern equatorial Africa.

13. C. PINNATIPARTITA O. Hoffm., Engler Bot. Jahrb. **30**:432. 1901.—Nyassaland (British Central African Protectorate) northward into German East Africa.

14. C. LUPULINA O. Hoffm., *loc. cit.*—Southwesternmost German East Africa.

15. C. WHYTEI S. L. Moore, Jour. Linn Soc. **35**:348. 1902.—Nyassaland. Too close to *C. pinnatipartita*.

16. C. NEUMANNII Sherff, BOT. GAZ. **76**:85. 1923.—Southern Abyssinia.

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A. Rich. Tent. Fl. Abyssin. 1:409. 1847; *Coreopsis callosa* Schz. Bip. *in* Schweinf. *et* Aschers. Enum. 284. Abyssinia.

C. PACHYLOMA var. INANIS Sherff, BOT. GAZ. **90**:386. 1930.—Abyssinia.

26. C. PRESTINARIA Schz. Bip. *in* Walpers *loc. cit.; Prestinaria bidentoides* Schz. Bip., *loc. cit.; Verbesina veris* A. Rich. Tent. Fl. Abyssin. 1:407. 1847; *Coreopsis prestinaria* f. *typica et* f. *latisecta* Vatke, Linnaea **39**:498. 1875.—Abyssinia.

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C. PRESTINARIAEFORMIS var. INCISA Sherff, BOT. GAZ. **90**:387. 1930.—Abyssinia.

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CHICAGO NORMAL COLLEGE
CHICAGO, ILL.

DISTRIBUTION OF TOTAL NITROGEN IN REGENERATION OF THE WILLOW

P. A. DAVIES

(WITH FIVE FIGURES)

Introduction

The correlation between growth and available supply of carbohydrates and nitrogen has been studied by various workers. BUTLER, SMITH, and CURRY (1), with data secured from experiments on apple trees, came to the conclusion that vegetative awakening (bud development) is correlated with translocation of reserve nitrogen to the growing point. KRAUS and KRAYBILL (8) found that vegetative growth and reproduction in the tomato depend to a large extent upon an available carbohydrate-nitrogen relationship. They also found a descending gradient of total nitrogen from the apex to the base. HARVEY (5) reported that, in shoots of the apple, relatively great chemical differences exist between tip and basal areas. Nitrogen is more abundant at the apex; carbohydrates at the base. The results of MURNEEK (9) point to nitrogen as an immediate limiting factor affecting the influence of correlation in the tomato plant. The fruits monopolize almost all the available nitrogen; and in plants which are low in nitrogen, a single fruit will inhibit vegetative development. When the fruit is removed, vegetative development continues. Recently Miss REID (10, 11, 12) has produced valuable results on the carbohydrate-nitrogen relationship with seedlings of tomato, wheat, and squash. Her results indicate that increased nitrogen increases the growth of stems and leaves, and in the low-protein seedlings more than in the high-protein seedlings; and that an increased supply of carbohydrates increases root response, especially in the high-protein seedlings.

Regeneration is but a growth process, so the carbohydrate-nitrogen relationship should hold equally as well for regeneration as for growth. Miss HICKS (6) has applied the results obtained by KRAUS and KRAYBILL, HARVEY, MURNEEK, REID, and others to regenera-

tion in *Salix viminalis*. She states that active respiration seems to supply energy to expedite the translocation of nitrogen upward and the flow of carbon toward the base. Prior to growth, a lower C/N ratio is established at the apex and a higher C/N ratio at the base. Shoots develop in the area of lowest C/N ratio (apex) and roots in the area of highest C/N ratio (base). Her observations do not always agree with her conclusions. The nitrate-infused cuttings failed to develop, while in the carbohydrate-infused cuttings shoot development was greater than in the control. The writer's work shows the distribution of total nitrogen in the early stages of regeneration and development in *Salix nigra*. Some of the conclusions agree with those of Miss Hicks, while others do not.

Materials and methods

In studying regeneration, it is desirable to obtain material in which regeneration and development take place rapidly without the use of nutrient solutions. Under such conditions, the power of regeneration and development is invested solely in the cutting, and is in no way influenced by outside nutritive materials. *Salix nigra* was found to be favorable for this study, because shoot development and root regeneration take place rapidly, and polarity under normal conditions is very distinct.

For each experiment an entire willow shoot was used. It is necessary to know the total nitrogen gradient of the entire shoot, so that when cuttings are made, the gradient of each cutting is known. The gradient was obtained by making total nitrogen analyses at intervals along the entire shoot. The remainder of the shoot was then cut into 6-inch lengths. The cuttings were suspended, either in a normal or an inverted position, so that the lower half of each cutting was in well aerated distilled water, which was changed daily. The cuttings were kept in a dark chamber at 25° C.

The amount of material used for each analysis varied with the size of the cutting. In large cuttings, 1.5-inch pieces were used; in small cuttings, 2–3-inch pieces. The pieces were divided lengthwise into quarters. Opposite quarters were used for dry weight determination and the remaining quarters for total nitrogen analysis. By using the opposite quarters, the possible error was reduced. For

dry weight determinations, the material was placed in an oven at 102° C. and allowed to remain until a constant weight was obtained. Because there was only a small amount of root and shoot material available, more constant results were obtained by using the entire amount for total nitrogen on a dry weight basis, rather than dividing it as was done with the cuttings. The results given for roots and shoots are from dry weight materials. The total nitrogen analyses were made by the Kjeldahl-Gunning method. The results are shown in milligrams of nitrogen per gram dry weight of the material. The total nitrogen of roots and shoots was adjusted to the dry weight of the bark.

Results

It was found in early tests that the total nitrogen per gram dry weight of the bark was greater than that of the wood, and that the

TABLE I

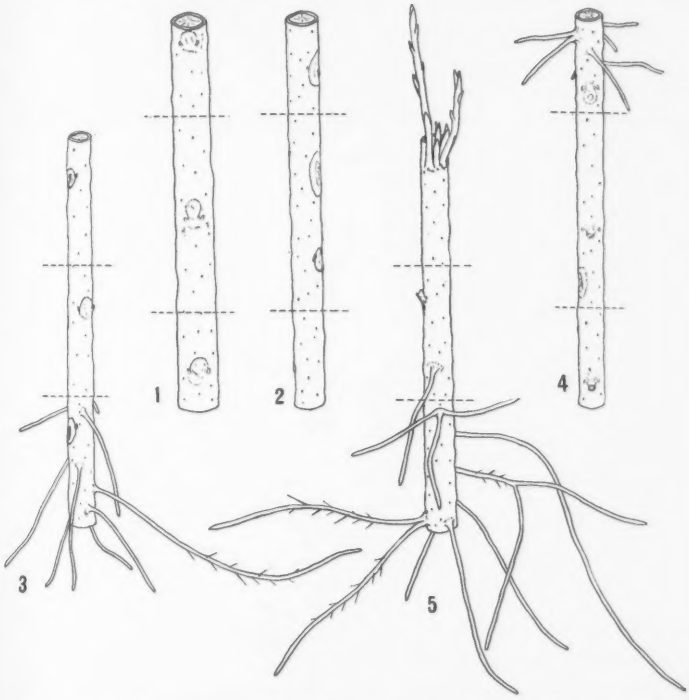
TOTAL NITROGEN ANALYSES OF CUTTINGS SHOWN IN FIGS. 1 AND 2

PART USED FOR NITROGEN DETERMINATION	NORMAL MG. N PER GM. DRY WEIGHT		INVERTED MG. N PER GM. DRY WEIGHT	
	Bark	Wood	Bark	Wood
Morphological apex..	15.0502	2.8330	15.7058	2.7309
Morphological base..	14.9859	2.7791	15.6129	2.6508

proportion of bark to wood became greater from the base to the apex, so that it was necessary to determine the wood and bark separately. The roots and shoots were also determined separately. In showing the gradient of total nitrogen, the total nitrogen of the roots and the shoots was added to the total nitrogen of the bark. This incurred a slight error, for the nitrogen of the shoots and the roots did not come solely from the bark, but a small amount from the wood. The error was small, however, so that it did not greatly affect the value of the results.

Table I shows the distribution of total nitrogen from cuttings shown in figs. 1 and 2. The total nitrogen analyses were made 8 days after the experiment was in progress. There were no visible signs of shoot or root development in either cutting. In both cuttings (nor-

mal and inverted), the morphological apices show larger amounts of total nitrogen per gram dry weight in both wood and bark than the morphological bases, although the differences are not large. The high



FIGS. 1–5.—Figs. 1, 2, cuttings after 8 days: 1, normal position; 2, inverted position (apical part above and basal part below dotted lines used for analyses). Figs. 3, 4, cuttings after 12 days: 3, normal position; 4, inverted position; both cuttings show strong root polarity at morphological base (apical part above and basal part below dotted lines used for analyses). Fig. 5, cutting in normal position, showing both strong shoot and root polarity (apical part above and basal part below dotted lines used for analyses).

total nitrogen at the morphological apex is due to the normal nitrogen gradient of the cutting. The results indicate that at this early stage, when changes prior to regeneration and development are taking place, there is little if any translocation of nitrogen toward the apex.

Tables II and III show analyses of cuttings shown in figs. 3 and 4, after the experiment had been in progress 12 days. Both cuttings show a strong root polarity at the morphological base. The buds were swelling, although no opening could be observed. The appearance of roots prior to shoot development is not an abnormal condition due to cultural methods, for GOFF (4), JONES (7), and CURTIS (2) found that in a large number of plants under normal conditions, roots appear before the shoots. The results show that when the total nitrogen of the roots is added to that of the bark, the gradient of

TABLE II

TOTAL NITROGEN ANALYSES OF CUTTING SHOWN IN FIG. 3

PART USED FOR NITROGEN DETERMINATION	MG. N PER GM. DRY WEIGHT			
	Bark	Roots	Total	Wood
Morphological apex..	17.6185	.....	.....	2.5049
Morphological base..	16.9351	0.6060	17.5410	2.4618

TABLE III

TOTAL NITROGEN ANALYSES OF CUTTING SHOWN IN FIG. 4

PART USED FOR NITROGEN DETERMINATION	MG. N PER GM. DRY WEIGHT			
	Bark	Roots	Total	Wood
Morphological apex..	17.4732	.....	.....	2.7055
Morphological base..	16.9095	0.1284	17.0380	3.0270

total nitrogen is from the morphological apex to the base, regardless of the position of the cutting. Analyses of the wood show that in the cutting with a normal position (fig. 3) the gradient of total nitrogen is also from the morphological apex to the base; but in the inverted cutting (fig. 4) the gradient is from the morphological base to the apex. This shows that at this stage of development in the inverted cutting there is a larger amount of total nitrogen per gram dry weight of the wood at the morphological base than at the morphological apex.

Table IV shows analyses of a cutting (fig. 5) with a well developed root and shoot polarity. The shoots develop in the area of highest total nitrogen per gram dry weight of the cutting, and roots regen-

erate in the area of lowest total nitrogen per gram dry weight of the cutting; although the results show only small differences in the amount of total nitrogen from the apex to the base.

TABLE IV

TOTAL NITROGEN ANALYSES OF CUTTING SHOWN IN FIG. 5

PART USED FOR NITROGEN DETERMINATION	MG. N PER GM. DRY WEIGHT				
	Bark	Shoots	Roots	Total	Wood
Morphological apex.....	15.9756	2.4527	.....	18.4284	2.5799
Morphological base.....	17.2040	.....	0.6410	17.8451	2.7022

CURTIS (2) concluded that normally very little, if any, food is translocated up the main stem to be used in shoot growth. DENNY and STANTON (3) have shown that the resumption of growth of the bud of the lilac does not depend upon the remainder of the plant, but is the result of conditions within the bud. The writer's results seem to coincide with those of CURTIS, DENNY, and STANTON, and show that changes prior to regeneration and development in cuttings of *Salix nigra* are not due to a rapid translocation of nitrogen from the base toward the apex.

Summary

1. Willow shoots develop in the area of highest total nitrogen per gram dry weight of the cutting; and roots regenerate in the area of lowest total nitrogen per gram dry weight of the cutting, in cuttings having a normal nitrogen gradient, suspended in a normal position, and with a well developed root and shoot polarity.

2. Analyses of material in the early stages of development seem to indicate that the initial changes prior to regeneration and development are not dependent upon the rapid translocation of nitrogen toward the apex.

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[*Accepted for publication June 6, 1930*]

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BRIEFER ARTICLES

PREPARATION OF COPY[1]

Manuscript

While the general presentation and organization of a paper must of course be left to the author's judgment, this brief article is prepared with the desire to help the prospective contributor to the extent that an editor can do so.

A simple, direct statement of facts, shorn of all unnecessary words, should be the contributor's goal for effective writing. It should be borne in mind that the paper is addressed to an audience of trained botanists, already conversant with the fundamentals of the science. Readers do not need to have general botanical terms defined, nor common botanical knowledge repeated. Some contributors, especially those with less experience, resort to much repetition in an effort to make their points clear, instead of presenting the information effectively in the first place. The majority of papers submitted to this journal would be greatly improved in quality by drastic cutting.

After the paper is typed and before it is submitted, it should be read and reread at intervals. This is the time to make revisions, not when the material is set up into type.

When historical data are presented, it is rarely necessary to review all the literature in detail, or to include all the literature citations to be found on the subject. Quotations from other papers should be employed only when really essential; usually the reference is sufficient.

Before the manuscript is typed, a copy of the BOTANICAL GAZETTE should be consulted, and the style followed as closely as possible, especially regarding the arrangement of literature citations, tabular material, and illustrations. Information regarding the maximum length of a paper and the amount of illustrative material accepted may be found on the inside front cover of the journal.

The following specific recommendations are not arbitrary, but are based upon reasonable requirements:

1. Use white paper of the regular typewriting size ($8\frac{1}{2}'' \times 11''$).
2. Double- or triple-space the entire manuscript, including literature

[1] A reprint of this article may be secured upon request to the editorial office of the BOTANICAL GAZETTE.

citations, figure legends (the descriptive statements or titles printed below illustrations), and footnotes.

3. Supply first sheets, not carbon copies.

4. Make all margins at least $1\frac{1}{4}''$ wide: the editor estimates the length of an article by the number of lines included, not by the number of pages involved.

5. Avoid combining different-sized sheets or using half-sheets. If it is found necessary, after the paper is typed, to insert additional material, use full-sized sheets even if they contain only a few lines.

6. Number the sheets in the top right-hand corner only.

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b. The author's initials or name and the subject of the paper should not be typed on each sheet. If the pages are numbered consecutively there is no risk of misplacement or loss.

c. No proof-reading signs or comments should appear in the margins. If it is wished to strike out a word or line, do this by an unmistakable stroke through the word or line, using black pencil or ink. Do not use a delete sign or the word "omit" in the margin. It is not necessary to include marginal notations regarding the insertion of illustrations; the reference in the text is sufficient guide for the printer.

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e. If the changes are many, the page should be retyped.

8. Leave to the editor the indication of the different kinds of type to be used throughout the paper. If the article is long, employ brief topical headings and subheadings, but do not underline them nor use capitals.

9. Spell out numbers beginning a sentence. As a rule, spell out the numerals from one to nine inclusive, using figures for higher numbers.

10. Treat **tabular material** as regular text, so far as page numbering is concerned, and insert it in the paper following the reference in the text. Unless it is impracticable on account of length, a table should be double-spaced, and the continuing text should begin on a fresh page. Since the setting up of tabular material is expensive, the contributor is urged to include only essential data, simplified as much as possible.

11. Employ **footnotes** only when really essential, and number them

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> 39. SATINA, SOPHIA, and BLAKESLEE, A. F., Studies on biochemical differences between (+) and (−) sexes in Mucors. Proc. Nat. Acad. Sci. **11**:528–534. 1925.

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The author must first decide whether his illustrations are to be prepared for use as plates or as text figures. Progress in the engraver's art has been so great during the last decade that excellent results may now be secured with the use of text figures, and this form of illustration has grown in favor with contributors. It has an advantage for the reader, who finds his illustration right at hand when reading the text. There is considerable economy to the publisher also: a full page of line drawings costs $23 if used as a plate; $5.30 if used as a text figure. Contributors are encouraged to prepare illustrations for use as text figures whenever possible.

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2. **Size of reproduction.**—The available space for text figures is 4 inches in width, and, including the legend, $6\frac{1}{2}$ inches in length. Illustrations for plates should be $5'' \times 7\frac{1}{2}''$ when reduced; that is, the proportion of the width to the length should be as 2:3.

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8. **Index lettering.**—It is most important to use printed letters and figures large enough to reduce with the rest of the illustration and retain their legibility. The smallest size used obviously should be the one considered in this connection. Sheets of printed figures and letters will be supplied by the editorial office upon request. Index letters should be mounted reasonably close to the object they designate.—THE EDITORS.

CURRENT LITERATURE

BOOK REVIEWS

Revision of the Chicago textbook

Recent publication of the revised edition of the Chicago textbook[1] again makes this volume available to students and teachers. The new edition appears in three separate volumes. The morphology text, Volume I, by the late JOHN M. COULTER, remains essentially the same as the earlier edition except for a 5-page bibliography of general literature on thallophytes, bryophytes, pteridophytes, and spermatophytes at the end of the book.

The physiology text, Volume II, has been thoroughly revised by C. A. SHULL. Although the chapter headings and much of the text in the original edition by C. R. BARNES have been retained, the revised edition has been improved by an expansion of more than 100 pages in subject matter, insertion of footnote citations to original literature, addition of a list of standard reference texts at the end of each chapter, and enlargement of the index. The new edition contains amplified discussions of soil moisture, mineral nutrients, osmotic phenomena, the cohesion theory, fat synthesis, enzymes, fermentation, and plant growth and movement.

The new subject matter describes recent advances in plant physiology in the same lucid style found in the original. The bibliographical references constitute a very valuable addition. They will greatly assist inquiring students in finding more information about topics cursorily treated in the text, and will at the same time familiarize them with the current literature of plant physiology. Although citations to foreign literature may not be a great help to beginners, they reveal the international character of scientific activity as well as the value of foreign languages in scientific work.

Although the text has been prepared for undergraduate use, it appears to the reviewer that the subject matter is advanced in character for college students pursuing an introductory course in botany. The extremely concise presentation gives the contents an enormous scope which beginners will find difficult to compass in its entirety; and though SHULL has done a great deal to improve the presentation of difficult subject matter, instructors who use the text in elementary courses will be obliged to simplify and elucidate the description of the more intricate physico-chemical processes. Recent changes in the character of college education and modern developments in the life sciences may also make it desirable for teachers in undergraduate courses to temper the scientific austerity of the book by frequent reference to plant physiological features of human interest.

[1] COULTER, J. M., BARNES, C. R., and COWLES, H. C., A textbook of botany, revised. Vol. I, Morphology. pp. viii+310. *figs. 618*. Vol. II, Physiology. pp. vi+307. *figs. 87*. American Book Company. New York. 1930.

The excellent stylistic composition suffers in only a few places from vagueness and the possibility of misconstruction. Botanists will, for instance, question the wisdom of referring to the cell wall as a membrane (p. 5) when later this term is used in another sense (p. 21). The discussion of imbibition (pp. 6, 7, 9), soil colloids (pp. 48, 50), and autumnal coloration (p. 128) hardly possesses the clarity requisite in an elementary text. Casual mention of suction pressure in a short paragraph at the end of the discussion of turgor and osmotic pressure (pp. 25, 26) might lead to confusion concerning the character and rôle of these forces. The concept of the isoelectric point (p. 48) is introduced abruptly and apparently with little justification as no attempt is made to develop its physiological significance. Mention of the photoelectric cell might have been included in connection with the discussion of the thermodynamics of photosynthesis (p. 228). The foregoing comments concern minutiae and probably express difference of opinion rather than criticism. SHULL has performed an excellent task in bringing this classical textbook of plant physiology up to date.

The Chicago textbook continues to be a masterful presentation of fundamental subject matter. Its terseness, accuracy, and scope will retain for it the preeminent position this text has so long enjoyed. On the whole, it appears that the new edition, like its predecessor, is especially well adapted for use at intermediate levels of instruction. Its appearance in separate volumes admirably adapts it for use in intermediate courses, and this form of the new edition suggests the publishers' recognition of this possibility. The revised edition has gained in excellence of presentation and printing, while the three volumes of smaller size add to its convenience and durability.—W. F. LOEHWING.

Plant physiological chemistry

There has long been needed a book summarizing the chemistry of the metabolic processes of the plant. There are several good plant chemistries on the market, but these are written largely from the chemical rather than the physiological point of view. There has been needed a volume giving the chemistry required for an adequate understanding of the vital processes of the plant, without drawing too largely on the mass information which the pure organic chemists have by their research accumulated in regard to the properties and reactions of the various organic compounds. This need has been adequately met by HARVEY'S recent book.[2] In the words of the author, "It is the purpose of this text to present the physiological-chemical mechanism of the vital processes of plants." No attempt is made to give a complete discussion of organic compounds; but only that chemistry is introduced which is thought to be needed to understand the life processes of the plant.

The book is divided into an introduction and six parts. The introduction consists of a discussion of the mechanism involved in the transformations of material. Catalytic action is discussed, and a treatment given of enzymes and their

[2] HARVEY, R. B., Plant physiological chemistry. pp. xix+413. *figs. 119.* Century Company. New York. 1930.

action. Part I consists of a discussion of the general metabolic processes of the plant. Among the subjects treated in this section are absorption, the inorganic nutrients, chemosynthesis, and the nitrogen cycle. Part II is a treatment of the carbohydrates and their uses in the metabolic processes of the plant. Part III discusses the fats, lipides, and waxes; and part IV, the proteins. Parts V and VI are devoted to photosynthesis and respiration. An interesting and valuable feature of the book is the inclusion of photographs of a number of men who have been leaders in the development of plant physiology, most of these being accompanied by quotations from their important publications. Most plant physiologists know all too little about the history of their subject.

Some will think that the author has at certain places been too arbitrary in the choice of a theory to explain a process, and will feel that some indication should have been given of other possible theories; but the author has considered it important to present the theory best fitting the facts, although it may be not without exception and it may be proved false in the future, rather than to confuse the student by presenting too much controversial material.

There is a well selected bibliography at the end of the volume, but the references are not specifically referred to by number in the text of the book. The author tried to avoid too profuse citation of literature, thinking that it confuses the student.

It is a difficult matter to summarize the chemistry of the plant's life processes, and the author has done his task well. All plant physiologists and those in fields using plant physiology as a tool will want at hand a copy of the volume.—S. V. EATON.

Self-sterility and hybrid sterility

Volume 21 of *Monographien aus dem Gesamtgebiet der Physiologie der Pflanzen und der Tiere* is a review of the problems of sterility by BRIEGER.[3] The brief introduction considers sterility as related to ontogeny, the heritability of sterility, and an explanation of the sense in which he uses the term "parasterility," a new term coined to obviate misunderstandings in the discussion of sterility phenomena. The term is used to designate "incompatibility," but in a broader sense than that used by STOUT in 1916.

The main part of the work deals with parasterility among the higher plants, first with reference to flower structure (dichogamy, hercogamy), and then with reference to pollen physiology. The latter section contains a general review of pollen physiology and fertilization, followed by consideration of self-parasterility accompanied by cross-fertility, cross-parasterility accompanied by self-fertility, incomplete parasterility, parasterility from heterostyly, and parasterility in case of species crosses. A brief summary concludes the pollen physiology section.

The last 100 pages of the book take up parasterility in animals, and in thallophytes and protista, with a final chapter of general conclusions. These

[3] BRIEGER, FRIEDRICH, Selbststerilität und Kreuzungssterilität. 8vo. pp. xii+393. Springer, Berlin. 1930. 33.8 RM, bound.

general conclusions deal with the problems of adaptation, inbreeding degeneration, and sexuality and parasterility.

There are 118 illustrations; and a literature list of over 700 titles, which indicates a thorough summary of the existing literature on sterility. Those interested in this field of biology will find the volume an interesting and valuable guide to a great body of facts.—C. A. SHULL.

Plant dispersal

How plants have traveled to all parts of the globe is a question of perennial interest to students of plant science. Answers to many phases of this universal question have been given by RIDLEY[4] in an encyclopedic volume of over 700 pages. The author has collected observations and records from many sources, as evidenced by the 500 citations of literature on the subject. To this he has added data from his own observations and from unpublished records of other naturalists.

The material has been organized under the main headings of dispersal by wind, by animals, by birds, by reptiles, by simple adhesion, by adhesion through special modifications, by adhesion due to viscid exudation, by human agency, and by mechanical dispersal. Under these headings subdivisions are introduced, based on plant families, genera, and species and also on a taxonomic organization of dispersing birds and insects. The index is one of the plant species concerned, but this together with a table of contents will make the varied contents of the volume readily available for reference. The book should prove a useful guide in a broad but widely explored field.—G. D. FULLER.

Plants of the Gold Coast

This semi-popular description of the plants of the Gold Coast, Africa, has been prepared by IRVINE[5] for use in the region indicated. It is unique in giving the native names of the plants, using for the spelling of these names an alphabet with half a dozen new characters foreign to English books. The major portion of the volume is devoted to non-technical descriptions of native plants designated by their botanical and their native names. The latter are often given in the dialects of four or five different tribes.

The interest of botanists in general will center in the descriptions of the vegetation, which comprises evergreen rain forest, deciduous forest, secondary evergreen forest, savanna forest, savanna, grass savanna, grassland, strand communities, and mangrove associations. There are also lists of plants used for various economic purposes.

The illustrations include some 50 excellent photographs, well reproduced, that serve to convey a vivid picture of the various plant associations.—G. D. FULLER.

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[4] RIDLEY, H. N., The dispersal of plants throughout the world. pp. xx+744. *pls.* 22. L. Reeve & Co. Ashford, England. 1930.

[5] IRVINE, F. R., Plants of the Gold Coast. pp. xxxix+521. *figs.* 69. Oxford University Press. London and New York. 1930. $1.75.

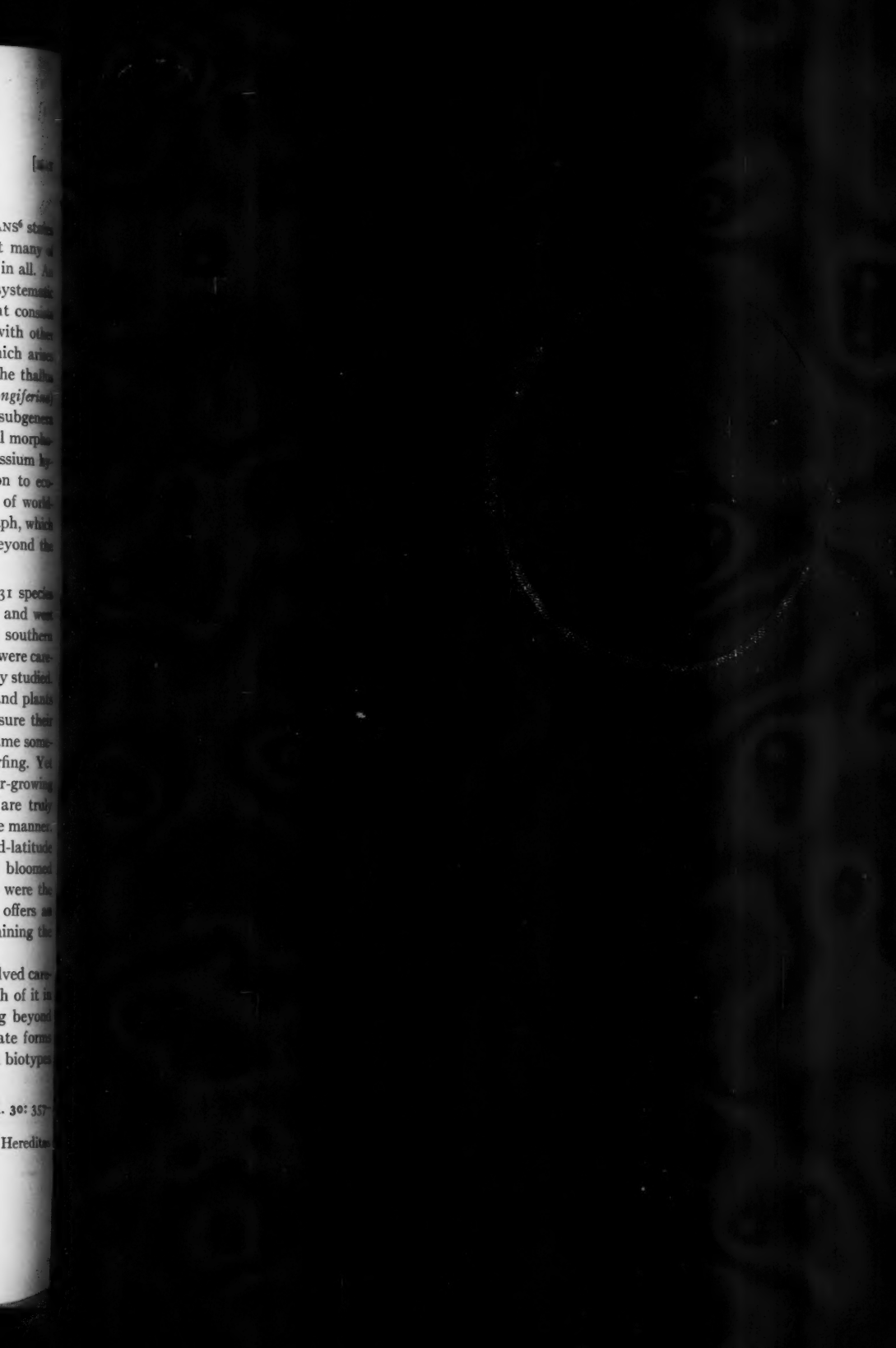
NOTES FOR STUDENTS

The lichen genus Cladonia.—A scholarly taxonomic study by EVANS[6] states that 45 species of *Cladonia* are now known in Connecticut, and that many of these are represented by a number of "forms," making a total of 163 in all. An illuminating account of the morphology of *Cladonia* precedes the systematic treatment of the individual species. It is shown that a *Cladonia* plant consists of two portions, the thallus or purely vegetative part homologous with other lichens, and the branched podetium or apothecium-bearing area which arises from the upper surface of the thallus or from the margin of one of the thallus scales. In the subgenus *Cladina*, to which reindeer moss (*Cladonia rangiferina*) belongs, the thallus is small and evanescent, but in the two other subgenera it may be long persistent. Keys to species make use, not only of usual morphological features, but in many cases employ color reactions with potassium hydroxide. Explanations of local distribution of species show attention to ecological details. Since the genus *Cladonia* and many of its species are of world-wide distribution (on all continents, including Australia), this monograph, which expresses the last word in lichen taxonomy, will be of service far beyond the bounds of Connecticut.—F. RAMALEY.

Climate and plant species.—Seeds or vegetative specimens from 31 species were collected by TURESSON[7] in different climatic regions of Europe and west Asia, and then cultivated together in an experimental garden in southern Sweden. The natural biotypes (forms, varieties) of each of the species were carefully noted and their persistence or modification in the garden critically studied.

Among summer-blooming species, plants brought from the north and plants from the south when grown together tended to retain in large measure their differences in stature, although it is true that the northern plants became somewhat taller and the southern plants showed a certain amount of dwarfing. Yet in the same plot of ground the northern plants were consistently lower-growing than those from the south, and bloomed earlier. These differences are truly genetic, for in any species transplants and seedlings behave in the same manner. Spring-blooming plants when moved north and south to an area of mid-latitude behaved differently as to time of blooming; those from the south bloomed earliest, those from the north came next, while the latest to bloom were the plants native to the region of the experimental garden. TURESSON offers an explanation of this phenomenon and discusses his methods of determining the geographic origin of horticultural forms.

The author's work was carried through a number of years, and involved careful handling of material in the garden as well as arduous travel, much of it in wild and forbidding territory. He is to be congratulated for showing beyond peradventure that in many species the mild-climate and severe-climate forms are not mere ecological variants, as might be assumed, but are instead biotypes of different hereditary nature.—F. RAMALEY.

[6] EVANS, A. W., Cladoniae of Connecticut. Trans. Conn. Acad. Arts Sci. **30**: 357–510. 1930.

[7] TURESSON, GÖTE, The selective effect of climate upon plant species. Hereditas **14**: 99–152. 1930.